RESPONSE OF NORTHERN RED-BACKED VOLE (*CLETHRIONOMYS RUTILUS*)

POPULATIONS TO A MAJOR SPRUCE BEETLE INFESTATION

IN THE COPPER RIVER BASIN, ALASKA

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A

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ABSTRACT

A spruce bark beetle (*Dendroctonus rufipennis*) epidemic in the Copper Basin of Alaska beginning in the late 1980's has infested over 200,000 ha of white spruce forests in the region. The impact of spruce beetle-induced habitat changes on the northern red-backed vole (*Clethrionomys rutilus*) was investigated using mark/recapture techniques for 2 field seasons. Vole abundance and recruitment was significantly greater on low versus heavily infested sites but a large vole survival response was lacking. Vole food resources and protective vegetative cover did not vary substantially in areas with different levels of spruce mortality. Male movement distances were influenced by sex ratio, and females appeared to respond to food resources (epigeous sporocarps). Beetle infestations alone did not influence vole movements, but female movement distances decreased when heavy infestation levels were coupled with female age and sporocarp availability. The impact of beetle infestations on red-backed vole populations in the Copper Basin appears to be relatively small.

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INTRODUCTION

Much work has been done detailing the response of wildlife to various disturbance agents. Research has been conducted in the boreal system on the response of microtines to fire (West 1982) and logging (West et al. 1980). Research on the microtine response to forest pest outbreaks has been conducted in temperate latitudes (Stone 1995), but there have not been published studies (but see Collins et al. 1998 unpublished report) investigating the microtine response to forest pest epidemics in the boreal system. A spruce bark beetle (*Dendroctonus rufipennis*) infestation starting in the late 1980's has impacted over 200,000 ha of spruce forests in the Copper River Basin located in south-central Alaska. Investigations within Wrangell-St. Elias National Park and Preserve have been conducted to document the impact of the infestation on forest structure and the understory vegetation response (Wesser et al. 1999). The red-backed vole is a critical species in the forest ecosystem and has been used as an indicator of forest health (Nordyke and Buskirk 1991). Through mycophagy, red-backed vole dispersal of ectomycorrhizal inoculum has been tied to conifer succession and regeneration (Terwilliger and Pastor 1999). Red-backed voles are also critical prey species for a diversity of predators including commercially important marten (Buskirk and MacDonald 1984). This project was conducted to answer questions regarding the impact of spruce beetle infestations on northern red-backed vole (*Clethrionomys rutilus*) populations in the Copper River Basin of Alaska.

Several studies have shown an increase in understory biomass and plant productivity due to an opening of the forest canopy following bark beetle epidemics in lodgepole pine (*Pinus contorta*: Stone and Wolfe 1996), and ponderosa pine (*P. ponderosa*: Korvaicic et al. 1985). Most research on spruce beetle epidemics in Alaska has taken place in white spruce (*Picea glauca*) forests on the Kenai Peninsula (Hard et al. 1983, Holsten et al. 1995). Kenai Peninsula infestations are often followed by the establishment of a thick layer of *Calamagrostis canadensis* (northern bluejoint grass)

cover (Holsten et al. 1995), however, this grass cover was not found in post-infestation forests in the Copper River Basin. A thick *Calamagrostis* layer can prevent the regeneration of young spruce (Holsten et al. 1995). Vegetation changes after beetle infestations will alter the habitat of resident wildlife. Specifically, understory vegetation cover can play a crucial role in providing protective cover for microtine rodents (Taitt and Krebs 1983).

Beetle infestations can change the forest structure by preferentially attacking larger trees (Hard et al. 1983, Holstein et al. 1995). The level of beetle-induced spruce mortality in Copper Basin white spruce stands was lower than levels found on the Kenai Peninsula (Collins et al. 1998) due to a prevalence of young spruce that were unaffected by the latest infestation. Also, our study areas in the Copper Basin had pre-infestation open canopies that were less affected by increased gap formation due to falling spruce trees than closed canopy forests. Due to the large variation in habitats where microtines live and the differences in species ecology, there is no set vole response to a particular disturbance agent. Beetle infestations in the Copper Basin provided an opportunity for a quasi-experiment, where red-backed vole population dynamics could be assessed in white spruce forests with varying beetle-induced spruce mortality levels. By assessing red-backed vole populations 5-10 years after infestations, the maximum response to changes in the forest vegetation established after infestations could be investigated.

There is a lack of information known about the response of small mammals to the habitat disturbance induced by forest pest epidemics. Unlike clear-cutting or fire, disturbance from beetle infestations in the Copper River Basin was relatively subtle. Knowledge of the red-backed vole response to major disturbance agents, such as bark beetle epidemics, is critical in understanding the forest dynamics and potential concomitant effects up the food chain. The information provided by this study contributes to knowledge of boreal forest ecology and the role of beetle infestations as disturbance agents in the Copper River Basin.

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Chapter 1*. Demographic response of northern red-backed vole (*Clethrionomys rutilus*) populations to a major spruce bark beetle infestation in the Copper River Basin, Alaska.

ABSTRACT

A significant cause of natural mortality of mature spruce trees in Alaska and other regions of North America is the spruce bark beetle (*Dendroctonus rufipennis*). The impact of beetle-induced habitat changes on small mammals is largely unknown. A mark/recapture effort was conducted on the northern red-backed vole (*Clethrionomys rutilus*) for 2 field seasons in the Copper River Basin of Alaska where infestations are widespread. Estimates of vole abundance, survival, and recruitment were produced in 3 locations that varied in their degree of beetle-induced spruce mortality. There was significantly greater vole abundance on low versus heavily infested sites (1997 $P < 0.01$, 1998 $P = 0.02$), but no differences between low and medium infested sites (1997 $P = 0.47$, 1998 $P = 0.36$) or medium verses heavily infested sites (1997 $P = 0.12$, 1998 $P = 0.48$). No vole survival differences were found across 3 locations with varied beetle-induced spruce mortality levels, but slight variation on replicate grids within each area was detected using habitat variables as group covariates. Percent beetle-killed spruce used as a group covariate revealed a slight decrease in vole survival with greater spruce mortality. Survival did vary across seasonal trapping periods in both 1997 and 1998. Vole recruitment was only estimated in the fall of 1997 and showed a larger contribution from both immigration and *in situ* reproduction in the low infestation area than the medium and heavy infestation sites. Vole food resources and protective vegetative cover did not vary substantially in areas with different levels of spruce mortality. Evidence from vole abundance and recruitment estimates suggests that beetle impact on red-backed voles may be negative, but results are more equivocal for vole survival effects.

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INTRODUCTION

A spruce bark beetle (*Dendroctonus rufipennis*) epidemic in the Copper Basin beginning in the late 1980's has infested over 200,000 ha of white spruce (*Picea glauca*) forests in the region (U.S. Forest Service 1998). The infestation has reached most white spruce stands in the region and continues to spread to remaining unaffected stands. Areas in the zone of beetle influence include private land (Chitna Village Native Corporation, Ahtna Native Corporation) and individual landowner properties, state land, and much of Wrangell-St. Elias National Park & Preserve. The pervasive influence of the current spruce beetle epidemic in the Copper River Basin has raised various concerns from land managers including the increase in fire potential, possible salvage logging efforts, and the impact on local wildlife. Our investigation addressed questions regarding the influence of beetle epidemics on the dynamics of red-backed vole (*Clethrionomys rutilus*) populations.

Bark beetle epidemics can change the forest structure by killing older and larger trees, thus lowering the average age and diameter of trees and allowing the release of smaller trees from competition (Veblen et al. 1991). Bark beetle epidemics open the canopy and allow more light to penetrate to the forest floor and enhance plant growth. An increase in understory biomass and plant productivity following beetle epidemics (genus *Dendroctonus*) has been shown for lodgepole pine (*Pinus contorta*) (Stone and Wolfe 1996) and ponderosa pine (*P. ponderosa*) (Kovacic et al. 1985). However, the impact on fauna of changes in forest structure and understory vegetation following beetle epidemics is not well understood.

Red-backed voles have been used as indicators of forest health due to their importance in the dynamics of forest communities (Nordyke and Buskirk 1991). Voles are potential dispersers and predators of forest seeds (Radvanyi 1970) and, through soil disturbance, can positively influence plant diversity and richness (Fox 1985). Through mycophagy, red-backed voles act as important spore dispersers for fungi that form ectomycorrhizae with the roots of vascular plants, critical to the survival (Clarkson and

Mills 1994) and regeneration (Terrwilliger and Pastor 1999) of conifers. Microtines are also a crucial food source for many predators including marten (Buskirk and MacDonald 1984) and great gray owls (Bull et al. 1989).

Microtine rodents respond differently to disturbance regimes depending on their ecology and the nature and degree of the disturbance agent. Habitat disturbance can cause demographic changes in microtine populations by altering the quantity and quality of available resources and local mortality rates (Paradis and Croset 1995). The response of microtine rodents to disturbances such as habitat fragmentation (Mills 1995, Johannesen and Ims 1996), logging (Hayward et al. 1999, for review see Kirkland 1990), and fire (West 1982) have been studied extensively, but the impact from habitat changes due to forest pest epidemics has only been investigated in lodgepole pine forests (Stone 1995).

Abundance of *Clethrionomys* has been found to respond positively to increased understory cover (Nordyke and Buskirk 1991) and food resources (Schweiger and Boutin 1995). A decrease in red-backed vole abundance after clear-cutting has also been related to a lack of suitable cover (Maser et al. 1978, Martell 1983). Stone (1995) indicated that an increase in understory vegetation cover in response to a bark beetle outbreak in lodgepole pine forests in Utah increased small mammal densities. Fruit from berry producing plants are an important *Clethrionomys* food (Martell 1981, Bangs 1984) and have been hypothesized to strongly influence their population density (West 1982). Sporocarps of mycorrhizal fungi also constitute a major food resource (Maser et al. 1978, West 1982) and have been used as an explanation for why *Clethrionomys* respond negatively to tree removal (Ure and Maser 1982, Mills 1995). Clear cutting practices eliminate symbiotic relationships of trees with mycorrhizal fungi and can lead to the disappearance of red-backed voles (Ure and Maser 1982, Mills 1995).

Disturbance regimes can range in size, type, and intensity, therefore, it is unsurprising that the patterns of red-backed vole response to disturbances are often unclear and contradictory. Following clear-cutting, red-backed voles have been shown to

both increase (Kirkland 1977, Verme and Ozaga 1981) and decrease (Martell 1983, Hayward et al. 1999) in abundance. When the intensity of the logging disturbance is lower than large scale clear-cuts, as in partial and/or patch cutting, the microtine response is harder to detect. The abundance of southern red-backed voles (*C. gapperi*) was not affected greatly by shelterwood harvesting (Von Trebra et al. 1998) or patch cutting (Martell 1983, Hayward et al. 1999), and northern red-backed voles (*C. rutilus*) showed little response to selectively logged forests (West et al. 1980). Red-backed vole response to a disturbance will depend on the composition of the stand before disturbance, the intensity of the disturbance, and the subsequent succession of the area (Martell 1983), therefore extrapolations from one system to another are equivocal.

Disturbance can change the quality of the habitat for resident small mammals by impacting their resource base. Habitat quality may be assessed when specific food and other resource requirements along with mortality risks are known. However, this information is difficult to attain for most species, especially resource generalists such as *Clethrionomys*. Often measures of habitat quality are based on demographic parameters (Van Horne 1983). Frequently abundance is used as the only measure of a response to disturbance which may be misleading when attempting to learn about habitat quality (Van Horne 1983). Relatively recently, survival rate estimation has been used to assess the quality of a habitat (Paradis and Croset 1995, Winker et al. 1995, Paradis 1995), and may provide greater insights to a population response than using abundance measures alone.

The objective of our study was to determine if the dynamics of northern red-backed vole populations are impacted by habitat changes induced by a major spruce beetle infestation. Northern red-backed voles inhabit a mosaic of forest conditions in Alaska. Their response to fire (West 1982) and logging (West 1980) has been investigated; however, the response of small mammals to spruce bark beetle infestations has not been investigated in boreal forests. We measured vole food availability, understory vegetation cover, and estimated vole abundance, survival, and recruitment,

and applied these measures as possible indicators of habitat quality in forests with varying levels of beetle-induced spruce mortality. We predicted spruce beetle infestations would influence the habitat of *C. rutilus* and this impact would be detected through a change in vole population parameters corresponding to the degree of beetle-induced spruce mortality. We also evaluated the robust design method for estimating vole population parameters.

METHODS

Study area

The study was conducted in the Copper River Basin (61° N, 145° W) located in south-central Alaska. Winters extend over 6 months and the average monthly temperatures range from a high of 13.4 °C in July to -21.0 °C in January. Average rainfall was 30 cm and average snow depths reach 165 cm. The vegetation community, as described in Gallant et al. (1995), was dominated by white spruce (*Picea glauca*) and black spruce (*P. mariana*) forests underlain by *Salix* and *Alnus* spp.; a short shrub layer of *Sheperdia canadensis, Ledum groenlandicum, Betula glandulosa, Vaccinium uliginosum*; a ground layer of *Geocaulon lividum, V. vitis-idaea, Empetrum nigrum, Arctostaphylos uva-ursi,* and moss (*Sphagnum* species). In 1997, 3 white spruce locations were selected along a 35 km stretch of the Richardson Highway 40 km south of Glennallen (Figure 1.1). Each location was designated as a treatment group defined as low (1-3%), medium (15-42%), or heavy (38-48%) according to the degree of sampled beetle-induced spruce mortality on three replicates within each treatment (see **Habitat characteristics** section below for sampling techniques).

Habitat characteristics

The point-centered-quarter method (PCQ) was used to assess spruce density, percent of beetle-killed spruce, and average diameter-at-breast-height (dbh) on each individual replicate (Higgins et al. 1996). On 50 randomly selected points on each

replicate grid, the distance to the nearest spruce tree within 4 quadrants around the point was measured while dbh and spruce condition were recorded. Mean spruce density on each replicate was calculated by taking the inverse of the squared mean distance between points (Higgins et al. 1996).

The understory vegetation cover and species composition were measured using 2, 50 m transect lines on each replicate employing the point-intercept technique to assess vegetation vertically from ground level to a height of 2 m at 1 m intervals (Higgins et al. 1996). Cover and PCQ measurements were conducted in August of 1997 and 1998.

Microtine food was assessed by sampling fungi/berry abundance on each replicate grid by counting and weighing (wet-weight) fungi (epigeous sporocarps with >1 cm caps) and berries (*Vaccinium uliginosum*, *V. vitis-idaea*, *Geocaulon lividum*, *Arctostaphylos uva-ursi*, *Empetrum nigrum*, *Rosa acicularis*, *Rubus chamaemorus*, *Rubus arcticus*, and *Sheperdia canadensis*) in 50 randomly selected 1 m^2 quadrats on each replicate (Johnson et al. 1995). This assessment was conducted at the beginning of August in 1997 and 1998 to coincide with the peak of berry and fungal fruiting.

Trapping procedures

Each treatment area contained 3 replicate 1 ha grids arranged in an 11 x 11 array of trapping stations with 10 m intervals. A single Sherman live trap (23x8x9 cm) was placed at each of the 121 stations. Traps were open for 5 days and checked 3 times daily except day 5 when the traps were checked and closed that morning. Traps were set with sunflower seeds and cotton bedding material and restocked after each capture. Captured voles were individually marked with a passive integrated transponder (PIT) tag (Schooley et al. 1993). Weight, capture location, and standard external reproductive data (males: testes scrotal or abdominal; females: pregnant, lactating, and vulva open or closed) were noted for each capture. Each treatment replicate was subjected to 4 trapping sessions separated by 16-30 day intervals beginning in late May-early June and ending in late August-early September in 1997 and 1998.

Data analysis: robust design

The trapping procedures were conducted according to Pollock's 'robust design' (Pollock 1982, Nichols et al. 1984). The robust design exploits 2 levels of sampling: primary sampling periods (e.g., monthly) and secondary sampling periods (e.g., daily) within each of the primary sampling periods. Closed population models of Otis et al. (1978) were used to estimate population size in each secondary sampling period. Closed models assume no demographic events occur during sampling. Cormack-Jolly-Seber (CJS) open population models (Cormack 1964, Jolly 1965, Seber 1965) were used to estimate survival between primary sampling periods. The main difference between the robust design and the use of CJS models alone is that instead of 1 capture occasion between survival intervals, more information from multiple secondary sampling events is used. Closed models permit abundance estimation under various assumptions of unequal capture probabilities, where survival estimation through the use of open models is robust to departures from unequal capture probabilities (Carothers 1973, Pollock et al. 1990). Although the robust design is a method befitting small mammal studies, we are aware of only 2 published investigation using this design (Paradis 1995, Wilson et al. 1999) aside from studies describing the method (Nichols et al. 1984, Kendall and Pollock 1992, Kendall et al. 1995) and its emigration/immigration estimation applications (Nichols and Pollock 1990, Kendall et al. 1997). The advantages of this approach to parameter estimation over open models alone are outlined in Kendall and Pollock (1992).

Abundance.--We used program CAPTURE (Otis et al. 1978, Rexstad and Burnham 1992) to generate abundance estimates for *C. rutilus* populations. Within each 5-day primary sampling period, capture data were transformed into capture histories (e.g., Otis et al. 1978) specifying the secondary sampling occasions when an individual was captured. Individual capture histories were stratified by replicate and, within each replicate, by sex. Closed models in CAPTURE incorporate 3 sources of unequal capture probabilities including individual heterogeneity, behavioral response, temporal variation, and all combinations (see Otis et al. 1978). A selection procedure uses a discriminant

function to rank the models for a given data set and estimates abundance according to the top ranking model. Individual trap mortalities were removed from the data pool before analysis and then added after the abundance estimates were produced from the capture histories of live animals (White et al. 1982:171).

The proper test statistic for examining abundance comparisons between treatments depends on whether capture probabilities were homogeneous within and between treatment populations (Skalski and Robson 1992:121). Testing for homogeneity of capture probabilities is needed to differentiate a treatment effect on abundance from variation in capture probabilities (Skalski and Robson 1992:112). Examining this assumption determines whether abundance estimates or catch indices should be used for tests. Catch indices are defined as the number of individual animals caught from the population (Skalski and Robson 1992:63, also denoted as M_{t+1} in Otis et al. 1978). Tests based on catch indices are preferred when equality of capture probability among treatments holds, because they allow greater power in detecting treatment effects by removing sampling uncertainty (Skalski and Robson 1992:125). Chi-squared tests from contingency tables were used to test the assumption of interpopulation homogeneity and determine the proper test statistic. Contingency tables were based on capture frequencies defined as the number of individuals captured exactly j times in t trap checks, $j = 1,2,...,t$ (Otis et al. 1978). The methods of Sokal and Rohlf (1981:780) were employed to pool test results across primary occasions.

Survival.--We used MARK, a program available on the World Wide Web (www.cnr.colostate.edu/~gwhite) (White and Burnham 1999), to generate vole survival rate estimates. Survival rates were estimated for the 16 to 30 day intervals between the four primary sampling periods in each year. Time intervals were standardized in MARK to produce 30-day survival rate estimates. We recognize that apparent survival, where permanent emigration and death *in situ* are not distinguished, was estimated.

Individual capture histories (see Lebreton et al. 1992), the basic input into MARK, were pooled within days to reduce daily temporal effects, combined across

primary periods, and stratified by replicate. This stratification allowed us to analyze the replicates as separate groups in MARK to investigate variation of survival and capture/recapture probabilities at the replicate level. Accidental trap deaths were coded as captured but not released on their last encounter.

Robust design models in MARK have 6 general parameters: survival rate, capture and recapture probability, temporary emigration and immigration rate, and abundance. Abundance estimates produced in CAPTURE are more flexible in modeling capture probability heterogeneity than those produced in MARK, hence CAPTURE abundance estimates were utilized. Emigration and immigration parameters were set to 0 throughout analysis.

Biologically plausible levels of variation were used in building models. Model notation (similar to Kendall et al. 1995) denotes variation at 2 levels: within primary period, and/or across primary periods. Models are designated as M_{α}^{β} where M denotes the parameter [survival (ϕ), capture probability (p), recapture probability (c), abundance (N)], α denotes within primary period variation, and β denotes variation between primary periods. α variation includes: variation between replicates (r), within daily secondary periods (sp) which is a feature particular to capture/recapture probabilities, and variation within a treatment group (T). β variation includes between primary period (C) and between year variation (Y). The absence of a particular script indicates constancy. For example, the model notation p_{sp}^{C} conveys variation in capture probability between secondary trapping occasions and primary periods, but constancy between replicates, treatments, and years.

A parameter rich or global model (Burnham and Anderson 1992) was created separately for each year. For this global model, survival rate was designed to vary by replicate and primary trapping period, and capture/recapture probabilities were structured

to vary by replicate, and within and between primary periods. Abundance was allowed to vary by replicate and primary period and this structure was maintained throughout the model building process to reflect natural variation in population size. This global model has the following notation:

$$\phi_r^C,\ p_{r\times sp}^C,\ c_{r\times sp}^C,\ N_r^C$$

Starting with this global model, subsequent models were constrained in a step-down approach (Lebreton et al. 1992). First, capture/recapture probabilities were simplified in each year separately while keeping the survival probabilities at the parameter rich state. Constraining capture probabilities first, provides the advantage of keeping as much power as possible for tests on survival parameters, which carry the most biological interest (Lebreton et al. 1992). Capture/recapture probabilities were simplified from the global model by pooling the data across primary periods, replicates, treatments, and secondary periods in a step-down approach (Figure 1.2). Comparisons were made between models to find the most parsimonious model (see model selection procedures below). The most parsimonious capture/recapture model structure was then maintained in subsequent survival rate modeling.

Survival rates were first modeled separately by year to determine sources of variation. Models were simplified by pooling primary periods, replicates, and treatments in a step-down fashion (Figure 1.3). Once variation in survival rates for each year was examined separately, yearly data were combined to explore interactions between years. Percent vegetation cover, spruce density, estimates of vole food availability assessed through berry and sporocarp counts, and percent of beetle-killed spruce measured on each replicate were incorporated into models as group covariates (see ***Habitat characteristics*** section for techniques used in vegetation assessments).

Estimates of survival rate parameters were produced from a model averaging procedure in MARK. A weighted average of survival rate estimates was calculated,

therefore, inferences can be based on more than a single model (Buckland et al. 1997). By averaging estimates over all models, model selection uncertainty is included in the estimate of precision of the parameters, therefore producing unconditional estimates of variances and standard errors (White et al. 1999). Model averaging techniques allow the precision of an estimate to have 2 variance components: 1) the conditional sampling variance, and 2) variation associated with model uncertainty (White et al. 1999). Partitioning the precision of survival rate estimates into these components was conducted in MARK.

Recruitment.--The components of recruitment, immigration and reproduction, are likely to be affected by different ecological or environmental factors. The capture-recapture data were analyzed to yield separate estimates of recruitment from immigration and *in situ* reproduction (Nichols and Pollock 1990). Two age classes were distinguished using a body mass criterion that corresponded with signs of reproductive maturity: >16 g = adult, <16 g = juvenile. Survival rate estimates were combined with closed model abundance estimates of juvenile and adult voles to obtain estimates of reproductive recruitment and immigration. Models for survival rate estimation were run in MARK separately by treatment under the robust design. Pairwise comparisons by treatment group of the partitioned recruitment estimates were conducted through Z-tests using the weighted mean of estimates across replicates.

Model selection procedures.--Model selection was based on the Akaike Information Criterion (AIC= -2 log likelihood + 2a, where a is the number of identifiable parameters) (Akaike 1973). The model with the lowest AIC represents the most parsimonious model that fits the data (Burnham and Anderson 1992, Lebreton et al. 1992). The principle of parsimony argues that a model should only retain parameters that are warranted by the data and that a model with too many parameters is undesirable (Lebreton et al. 1992). AIC adds a penalty for each parameter added to the model encouraging parsimonious models. Testing the importance of a given parameter structure can be accomplished by

comparing the AIC of differing models (Paradis and Croset 1995, Johannesen and Ims 1996). The AIC can be used to compare models that are not nested, without having to perform specific tests such as likelihood ratio tests (Anderson and Burnham 1994).

RESULTS

Habitat characteristics

Measured beetle-induced spruce mortality exhibited variation within our treatment areas with the low infestation site differing markedly from the other 2 sites (Figure 1.4). Spruce density samples on each replicate varied slightly across replicates and treatment areas (Figure 1.5). Average spruce dbh measured on replicates indicate that trees on the low infestation grids were smaller than the other treatment areas (Figure 1.6). This dbh variation can be attributed to a larger contribution of saplings in low infestation treatment areas due to greater regeneration on these grids.

The thickness of understory vegetation cover did not appear to vary greatly between treatment areas, but was slightly greater in the heavy treatment area (Figures 1.7-1.12). Species composition varied across treatments and slightly within treatments (Figures 1.7-1.12). The low treatment area had the only incidence of *Alnus* spp. and *Betula glandulosa* in the samples. The medium treatment contained a larger contribution from *Sheperdia canadensis* and *Arctostaphylos uva-ursi* than the other areas, while the heavy treatment area had more black spruce and *Salix* spp.

Sampled berry availability showed variation in species composition and quantities measured between replicates within a treatment area but showed no obvious trends across treatment areas or years (Figure 1.13). Weight of sampled sporocarps also showed variation within treatment areas in 1997, but samples indicated a low availability in 1998 across replicates and treatment areas (Figure 1.14).

Abundance

The northern red-backed vole (*Clethrionomys rutilus*) was the most common small mammal trapped, comprising over 95% of all captures. Over the course of the

study 1321 northern red-backed voles were captured on 7808 occasions during the snow free periods of 1997 and 1998. *Microtus oeconomus*, *Microtus xanthognathus*, *Synaptomys borealis*, and *Sorex* spp. were captured infrequently and were not used in separate analyses.

Tests for interpopulation homogeneity of capture probabilities indicated that there was homogeneity in *C. rutilus* capture probabilities both within and between treatments (case 3 in Skalski and Robson 1992:123) in all primary trapping sessions in 1997 and 1998. Homogeneity was also found between years within a given treatment area. These results allowed catch indices to be used to test for population size differences between treatments.

C. rutilus abundance estimates (Figure 1.15) indicated that populations exhibited interannual growth on all replicates in both years over the four primary sampling periods. Abundances were lower in 1998 on all replicates (Figure 1.15). Tests pooled across primary periods showed vole numbers were significantly higher in 1997 than 1998 within a given treatment area for the low ($P < 0.01$) and medium ($P = 0.02$) treatments, but not significantly different for the heavy treatment area ($P = 0.06$).

Generally, vole abundance was lower within treatment areas as the level of beetle-induced spruce mortality was higher, although the trend was more pronounced in 1997 when abundances were higher overall (Figure 1.15). Results when catch indices were pooled within treatments and test results for all four primary trapping periods were pooled (Sokal and Rohlf 1981:780) showed significantly greater red-backed vole abundance on low versus heavy beetle infestation treatments (1997 $P < 0.01$, 1998 $P = 0.02$), but no differences between low and medium (1997 $P = 0.47$, 1998 $P = 0.36$) or medium and heavy treatment areas (1997 $P = 0.13$, 1998 $P = 0.48$).

A diversity of closed models were selected to estimate population size. For both sexes in 1997, the model where the probability of capture varied by individual heterogeneity (M_h) was most frequently chosen (Table 1.1) from the array of closed

models (see Otis et al. 1978). This differed from 1998 where the top model for females included variation in time and individual heterogeneity and for males displayed a more even range of capture probability variation (Table 1.1). The null model (M_o), which assumes no variation in capture probabilities, was selected more often in 1998 than in 1997 (Table 1.1). This was likely due to the lower number of individuals captured in 1998 which can lead to an inability to detect variation in capture probability (Menkens and Anderson 1988).

Survival

The temporary emigration and immigration parameters were set to 0 throughout our analysis. Temporary emigration occurs when an individual is caught in the first or second primary period, not caught in a subsequent period, and then captured again. This occurred infrequently (2/404 individual capture histories). Therefore, virtually all emigration in our data set was permanent. For the "no emigration model", if the temporary emigration parameter is set to 0, immigration must also be set to 0 because there are no individuals allowed to temporarily emigrate to provide a source of immigrants back into the population (White and Burnham 1999).

Model selection based on the lowest AIC indicated that vole populations in both years exhibited similar variation in capture/recapture probabilities (Table 1.2). The favored model for both years allowed capture/recapture probabilities for replicates to be pooled within treatments and remain constant across secondary periods, thus having variation among treatment groups and primary trapping periods (p_T^C , c_T^C). This capture/recapture structure was used in all subsequent survival rate analyses.

The question of whether there was a treatment effect on survival rates was investigated by comparing the model where survival varies by treatment area (φ_T) with models that do not have a location component such as the model with constant survival (φ) or where survival varies temporally in primary trapping periods (φ^c). For both years, the best fitting model warranted separate estimates of survival across primary trapping

periods but not between treatments (Table 1.3).

Adopting model φ^c to be the most parsimonious model for each year, an interaction between primary trapping period and year improved the model (Table 1.4). Modeling 1997 survival rates as a positive linear trend further improved the model (Table 1.4). The only habitat group covariate that improved the model was spruce density (Table 1.5), which produced a slight negative response in survival as a function of increasing spruce density (β = - 4.3, SE = 2.3). Habitat group covariates of percent beetle killed trees, vegetation cover, and microtine food availability (berries and sporocarps) failed to improve the survival model (Table 1.5) but were close to the top model thus demonstrating an ability to detect variation at the replicate level.

Apparent survival rate estimates produced from a model averaging procedure revealed vole survival was much lower in spring of 1997 than in 1998 (Table 1.6). The percent variation associated with model uncertainty in survival rate estimates was relatively low across all replicates and years (Table 1.6). Estimates in 1997 showed a typical increase in survival as the breeding season progressed with peak survival in the late summer period (Table 1.6).

Recruitment

The estimation procedure that partitions recruitment into components of *in situ* reproduction and immigration (Nichols and Pollock 1990) requires the assumption that the time interval between successive primary sampling periods allows for the transition of juveniles to the adult class. Only the last interval of our study was sufficiently long (30 days) to satisfy this assumption. Only 1997 data had sufficient captures of juvenile individuals to allow for partitioning into the representative contributions of *in situ* reproduction and immigration.

Across all replicates, the contribution of recruitment from immigration was greater than reproduction and generally followed the trend of abundance differences between the treatments where immigration estimates were highest on the low treatment,

intermediate on the medium treatment, and lowest on the heavy treatment (Figure 1.16). The low beetle infestation treatment, with its higher vole abundances, also had larger recruitment values, but the contribution from immigration and *in situ* reproduction were dissimilar. The weighted mean of the immigration estimates on the heavy treatment was significantly less than on the low ($P < 0.01$) and medium treatments ($P < 0.01$), but not different between the low and medium treatments ($P = 0.13$). The reproduction component of recruitment generally followed the same trend as immigration (Figure 1.16). *In situ* reproduction estimates on the low treatment were significantly greater than on the medium ($P = 0.03$) and heavy treatment areas ($P = 0.03$), but there was no difference between the medium and heavy treatment areas ($P = 0.8$).

DISCUSSION

We investigated the impact of a spruce beetle infestation on the demography of the northern red-backed vole. We found that high levels of beetle-induced spruce mortality may be negatively affecting vole abundance, a result contrary to the small mammal response to mountain pine beetle epidemics in Utah lodgepole pine forests (Stone 1995). If beetle-induced habitat changes are creating a lower quality habitat for *C. rutilus* in the Copper River Basin, survival rates are perhaps the best assessment of habitat quality (Van Horne 1983, Paradis and Croset 1995). Through our modeling techniques, we failed to detect a beetle-induced treatment effect on red-backed vole survival when treating the dependent variable as categorical (low, medium, and heavy). Our inability to detect survival differences may be due to a small sample size or a lack of large understory vegetation response to beetle outbreaks in this region (Wesser et al. 1999) that would manifest itself in a treatment effect. *C. rutilus* is found in every major forest type in Alaska (West 1982) and may be well adapted to habitat changes or show little response to low level disturbances. We evaluate the robust design method for estimating microtine population parameters as well as the application of estimated

demographic parameters in reaching conclusions about *C. rutilus* response to spruce beetle infestations in the Copper River Basin, Alaska.

Habitat characteristics

Beetle infestations in the Copper Basin prompted investigations of possible effects on the flora and fauna. Pre-infestation information would have aided in determining beetle influence on species composition and vegetation cover differences on our study sites, however, these data were not available. Cover did not vary greatly across our treatment areas (Figures 1.7-1.12). The large invasions of *Calamagrostis* grass seen following beetle epidemics on the Kenai Peninsula were not seen in our study areas in the Copper Basin or in other areas in the region (Wesser et al. 1999) (see Gramanoids in Figures 1.7-1.12). A thick *Calamagrostis* layer would provide improved cover protection for voles and possibly favor *Microtus* spp. that prefer grassland habitats.

Other forests attacked by beetle epidemics sustained tree mortality at much higher levels (e.g., >90% in lodgepole pine forests, Stone 1995) than those found on our study sites. Low levels of spruce mortality coupled with an open canopy may account for a lack of understory growth following beetle epidemics in our study. Large berry/sporocarp and understory vegetation cover differences across our treatment areas were not found. We were able to tie an increase in survival to an increase in berry/sporocarp availability and greater cover (see **Survival and recruitment** discussion below), but the minor differences in vole food and cover measurements across treatment areas were reflected in only slight survival differences (Table 1.6).

Abundance

C. rutilus population abundance estimates at the end of the summer ranged between 41 (SE = 3.8) and 101 (SE = 9.1) individuals per hectare grid across all treatment populations in 1997 and between 20 (SE = 0.88) and 47 (SE = 9.6) in 1998 [although one replicate in 1998 had an unusually small population size of 8 (SE = 0.04) at the end of the summer]. These estimates are generally comparable to *C. rutilus* population sizes found

in interior Alaska black spruce forests (West 1982, Whitney and Feist 1984), birch forests (Whitney 1976), and white spruce forests of southwestern Yukon Territory (Gilbert and Krebs 1991).

C. rutilus abundance estimates were notably smaller in 1998 than 1997 across all three treatment areas. This suggests the occurrence of a regional event negatively affecting *C. rutilus* populations in the Copper Basin between 1997 and 1998 that might be attributable to factors believed to influence multiannual fluctuations of microtine populations. Weather data taken from the Tonsina, AK weather station (www.wrcc.dri.edu:80/cgi-bin/cliMAIN.pl?aktons) dating from 1962 show near average temperatures and precipitation during 1997 and 1998. Snowfall in 1997-1998 was normal but snowfall in the winter of 1996-1997 was the 4th lowest on record. However, vole numbers in the spring of 1997 were higher than in 1998 (Figure 1.15), suggesting that this lack of insulating snow cover did not have a strong negative impact on vole populations. Normalized difference vegetation index (NDVI) measures of the vegetation phenology in the Copper Basin indicated that 1997 was a longer growing season than 1998 (Markon 1999). This might have contributed to improved food and/or microclimate conditions for voles which could have influenced vole abundances in 1997. Indeed, an important vole food, sporocarps, were scarce in 1998 compared to 1997 (Figure 1.14). Qualitatively, sampled berry availability showed large variation between replicates within a treatment (Figure 1.13) and may not have played as large a role in influencing vole dynamics across treatments as the availability of sporocarps. Other factors could have added to lower vole numbers throughout 1998 trapping periods such as greater predation pressure, or habitat characteristics that were not measured.

It is unclear whether *C. rutilus* exhibit cyclicity in Alaska (cyclic: Pruitt 1968, Fuller 1969, noncyclic: Whitney 1976, West 1982). Contrary to Whitney (1976), West (1982) and our study show populations undergo a marked annual cycle with variable peak fall densities. Evidence of peak fall densities occurring at 3-4 year intervals requires long

term data sets and may be evident for *C. rutilus* in North America (Gilbert and Krebs 1991).

Abundance estimation techniques.--The closed models of Otis et al. (1978) are flexible, incorporating 3 potential sources of variation in capture probabilities, and thus permit robust estimation of abundance. Menkens and Anderson (1988) argued that the Lincoln-Peterson estimator provides abundance estimates with lower bias and variance than closed models except when there is a behavioral response or individual heterogeneity in capture probabilities. In our data, 86% of the closed model estimates of male and female abundance had either a behavioral and/or individual heterogeneity component to the modeled capture probabilities. Abundance estimates produced from open CJS models are negatively biased in the presence of heterogeneous capture probabilities (Nichols et al. 1984, Carothers 1973). Enumeration techniques such as 'minimum number known alive' assume trapping efforts ensure all individuals in a population will have a capture probability equal to 1, and therefore may lead to biased estimates (Nichols and Pollock 1983, Jolly and Dickson 1983). We believe that utilizing closed probabilistic estimators is the preferred method of abundance estimation due to their flexibility of capture probability modeling, especially considering the degree of behavioral and individual heterogeneity in capture probabilities found in our study.

The most widely used test for closure is implemented in CAPTURE (Otis et al. 1978) which computes the test assuming the model where capture probabilities vary by individual heterogeneity (M_h). Restricting the closure assumption under only one form of capture probability variation (M_h) allows for an excessive type I error rate in the presence of time or behavioral capture probability variation (White et al. 1982). New methods to test for closure under time specific data (Stanley and Burnham 1998) suffer similar shortcomings. We observed a wide range of capture probability variation (Table 1.2) and would falsely reject closure frequently when assuming only one type of capture probability variation. Therefore, until a more comprehensive closure test is created, we

believe that closure needs to be assessed from a biological standpoint. Keeping secondary capture periods to less than 5 full days allows the population to be considered closed for the purposes of abundance comparisons.

Tests for homogeneity of capture probabilities are necessary before using catch statistics to compare population size (Skalski and Robson 1992). Enumeration techniques employing catch statistics are often used to assess population size for small mammal studies (Taitt and Krebs 1983, Desy and Batzli 1989) but rarely test for inter-population homogeneity. Forest habitat changes have been found to influence capture rates in small mammal studies (Perry et al. 1977). Without testing this interpopulation homogeneity assumption, one implies that either treatment effects do not influence capture probabilities among compared populations or that abundance is completely enumerated. Skalski and Robson (1992) outline methods employed in our study for abundance comparisons that overcome these problems.

Survival and recruitment

Survival rates increased over the course of the summer in 1997 (Table 1.6). Low spring survival and high fall survival have been shown previously for *C. rutilus* in Alaska (Whitney 1976, West 1982). The high spring survival found in 1998 might be attributed to abundant food resources, such as berries left over from the previous year, that can become scarce in June and July (West 1982) or may have been influenced by a small sample size in the first trapping session. Our berry/sporocarp sampling occurred in August, therefore, possible vole food abundance or scarcity at the beginning of summer cannot be addressed from our sampling.

Sex specific survival models were constructed in 1997 when capture data were most plentiful and failed to reveal a treatment effect on survival for either sex. We did not choose to stratify the data according to age class outside of recruitment analysis because juveniles (<16 g) were caught relatively infrequently, especially early in the trapping season, and additional parameterization of the models by sex or age would have led to

parameter identifiability and computational problems (Paradis and Croset 1995).

Population size was significantly lower in the heavy beetle infestation treatment compared to the treatment with low spruce beetle activity (1997 $P < 0.01$, 1998 $P = 0.02$) (Figure 1.15). This suggests a negative influence of high beetle-induced spruce mortality on voles but it may be misleading to rely solely on population size measurements to assess a population response and/or habitat quality (Van Horne 1983). If spruce beetle effects are negatively impacting the red-backed vole community by making the habitat sub-optimal, one might expect a higher turnover of individuals in this lower quality habitat (Van Horne 1983, Winker et al. 1995). Turnover rates can be assessed by considering the combined contribution of mortality and permanent emigration. Apparent survival, therefore, is a good assessment of this dynamic. When we look at models with a lower AIC that are structured to exhibit a treatment component on apparent survival, survival rates are indeed lower in treatments with higher beetle infestation in 1997, but this trend is reversed in 1998 when data are more sparse. Without support from survival rate differences, we are able to make only limited inferences concerning habitat quality defined by abundance differences.

We did not detect a beetle-induced treatment effect on vole survival in either year (Table 1.3). The homogeneous estimation of *C. rutilus* survival rates across treatment populations suggests variation in predation, competition, emigration, or parasite/disease pressure was not appreciably different across treatment areas, or that the sample size was not sufficient to detect survival differences across treatments. We failed to detect survival differences across replicates or treatments (Table 1.3). Through evidence using group covariates, however, survival rate variation was detected at the replicate level (Table 1.6). Habitat characteristics on each replicate employed as continuous covariates improved the model (spruce density: Table 1.5) or showed adequate explanatory power by having AIC values near the top models (Table 1.5: % beetle-killed spruce, vegetation cover, berry and sporocarp counts). Berry and sporocarp covariates induced slightly

higher survival rates as they became more abundant (berries: $\beta = 0.002$, SE = 0.03, sporocarps: $\beta = 0.03$, SE = 0.04). Survival increased as vegetation cover increased ($\beta = 0.02$, SE = 0.07), and decreased with increasing levels of beetle-induced spruce mortality ($\beta = -0.46$, SE = 0.47) revealing some evidence that infestation impacts are negatively affecting vole survival. When beetle infestation was treated as a categorical variable, a treatment effect on vole survival was not detected, but the models incorporating beetle infestation as a continuous covariate showed variation in vole survival was indeed present and detectible across replicates, although the effect on survival was small.

Recruitment estimates can also clarify habitat quality differences across treatments. By partitioning recruitment into immigration and reproduction components, we examined the nature of population growth dynamics. Immigration estimates across treatments appear to be a direct reflection of population size differences (Figure 1.16). This suggests the area surrounding each replicate is contributing individuals to the trapping areas generally in proportion to the estimated population size on the trapping grids. Reproductive recruitment also had a greater contribution on the low infestation treatment than the other treatment areas (Figure 1.16). The low treatment seems not only able to support a larger population size than the other areas, but also able to support greater numbers of reproductive females (average of 29 versus 24 and 19 individuals on the medium and heavy treatments respectively), greater *in situ* reproduction, and possibly to allow greater numbers of juveniles to remain on the grids. A more favorable environment may allow for greater recruitment on areas with low versus high spruce mortality.

Goodness-of-fit test.--We did not conduct a goodness-of-fit test (GOF) to evaluate the fit of the global model (Burnham and Anderson 1992) in our survival analysis. The robust design does not produce deviances that allow GOF testing because models are not in the exponential family (White and Burnham 1999). Historically when GOF tests are conducted in small mammal studies the contingency tables for the tests often have

insufficient data (cell frequencies < 2) (Johannesen and Ims 1996) or analysis proceeds even though the global model fit is rejected (Johannesen and Ims 1996, Paradis et al. 1993, Nichols et al. 1984). Through model averaging, model selection uncertainty is included in the precision of the estimates. Using a series of models for estimation aids in overcoming a lack of fit of one model used individually for estimation. The percent variation associated with model uncertainty was relatively low for survival rate estimation (Table 1.6). Therefore, we are confident that the array of models constructed adequately reflect our ability to determine the sources of variation present in the data.

Conclusions

Variation in vole population dynamics in different locations always exist if adequate sampling is achieved (Skalski and Robson 1992:76). Although in this study, a beetle-induced treatment effect on *C. rutilus* survival was not detected, implications from the use of habitat variables used as group covariates revealed that variation in the various trapping grids was present (Table 1.5). The habitat characteristics appeared to have more explanatory power in detecting differences in survival across sampling areas (Table 1.5) than our search for a beetle-induced treatment effect. When percent beetle-killed spruce was used as a continuous covariate in survival models, within-treatment heterogeneity in red-backed vole survival showed voles responded negatively to increased spruce mortality but the effect was modest (Table 1.6).

Abundance and recruitment differences suggest that areas with low levels of beetle infestation may be higher quality habitats due to greater contributions from both on site reproduction and immigration. A much greater recruitment contribution from immigration (Figure 1.16) reflects the dispersal dynamics of this species. Greater knowledge of dispersal rates and distances moved for red-backed voles in forests with different beetle infestation levels could aid in understanding their response.

Populations of *C. rutilus* in Alaska are found in successional and mature forests (West 1982) and tundra habitat (Martell and Fuller 1979). Historically, habitat

disturbance from fire, wind, floods, spruce-killing pests, or other causes may have provided selection pressures that allowed *C. rutilus* to adapt to various forest types and ages, and hence their demography may remain relatively unaffected or only show small changes due to low levels of disturbance. We found a modest negative impact of beetle-induced spruce mortality reflected in abundance, survival, and recruitment estimates of red-backed voles. Much broader studies in terms of sampling scale (Hayward et al. 1999) and a more comprehensive look at the demographic responses at various time scales after beetle infestations are needed to fully understand the influence of beetle disturbance on *C. rutilus* populations.

MANAGEMENT IMPLICATIONS

Results from our study suggest that northern red-backed voles are less abundant in forests with a large percentage of beetle-killed spruce. This negative impact would have concomitant effects up the food chain, however, this response is highly variable. Red-backed vole populations display large interannual variation in population size (Gilbert and Krebs 1991), and we found significant differences in abundance between years within treatment areas. However, there was no interaction between abundance and year across our treatment areas, which indicates that interannual fluctuations in vole abundance can be assessed by surveying forests with any level of beetle infestation. This conclusion should not be extended to the entire Copper Basin or other regions. Forests on our study sites had open canopies before the latest beetle infestation, and beetle-induced spruce mortality was under 50%. This level of beetle damage is lower than that found in lodgepole pine forests where tree mortality over 90% was common, forest canopies were closed prior to infestation, and the microtine rodents displayed a positive response to beetle damage (Stone 1995). Forests more similar to these may be present in the Copper Basin, therefore, caution must be taken when extrapolating our results to forests that are structurally distinct.

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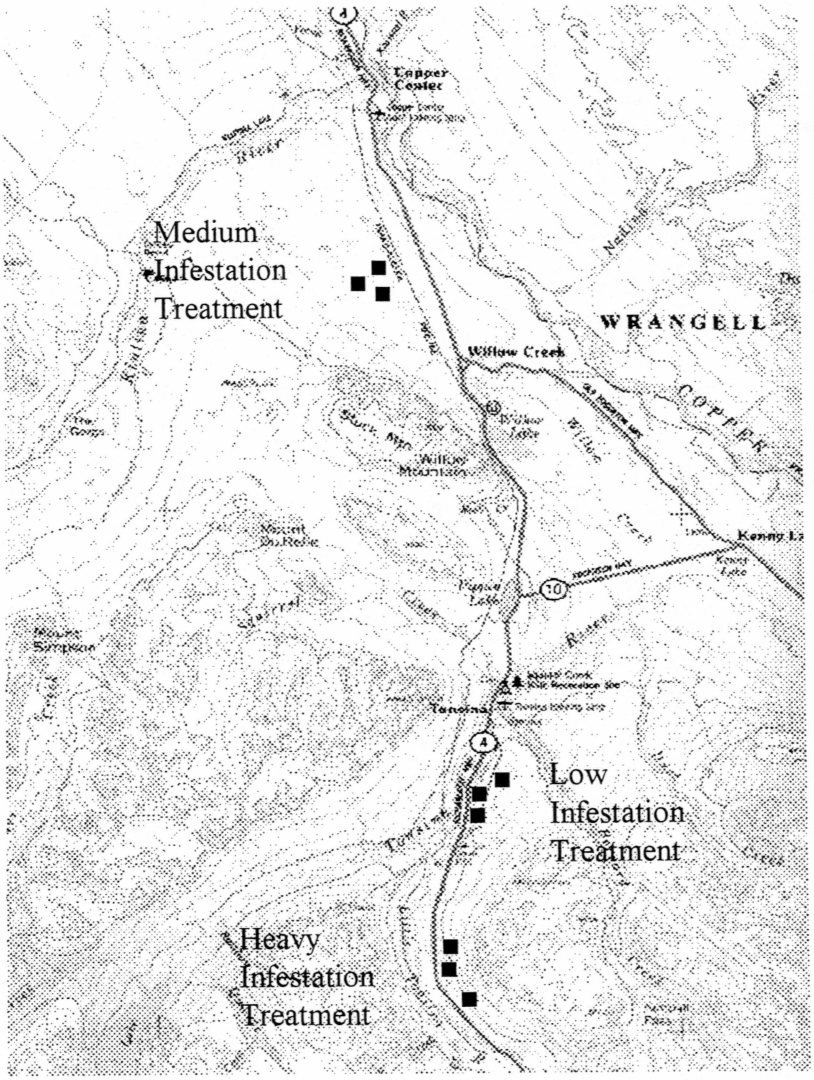

Figure 1.1. Study area map of the 3 beetle infestation treatment areas and individual grid positions from a topographic map of the Richardson Highway/Edgerton Highway cutoff region in the Copper River Basin, Alaska.

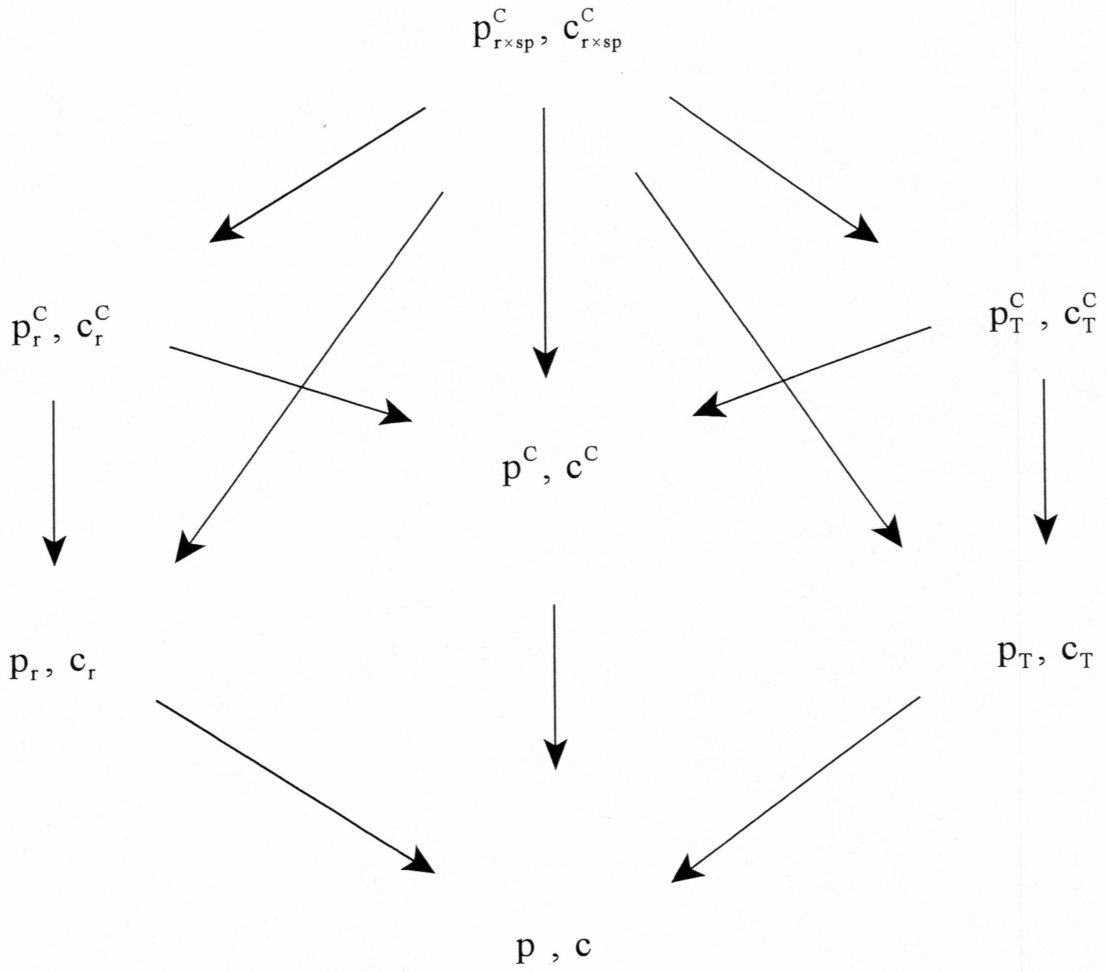

Figure 1.2. Hierarchical model diagram depicting *Clethrionomys rutilus* capture(p)/recapture(c) structures for models run separately by year under the robust design. Scripts define the type of variation: C = primary trapping period, r = replicate, sp = secondary trapping period, T = treatment. The arrows indicate decreasing levels of complexity and nested relationships between models.

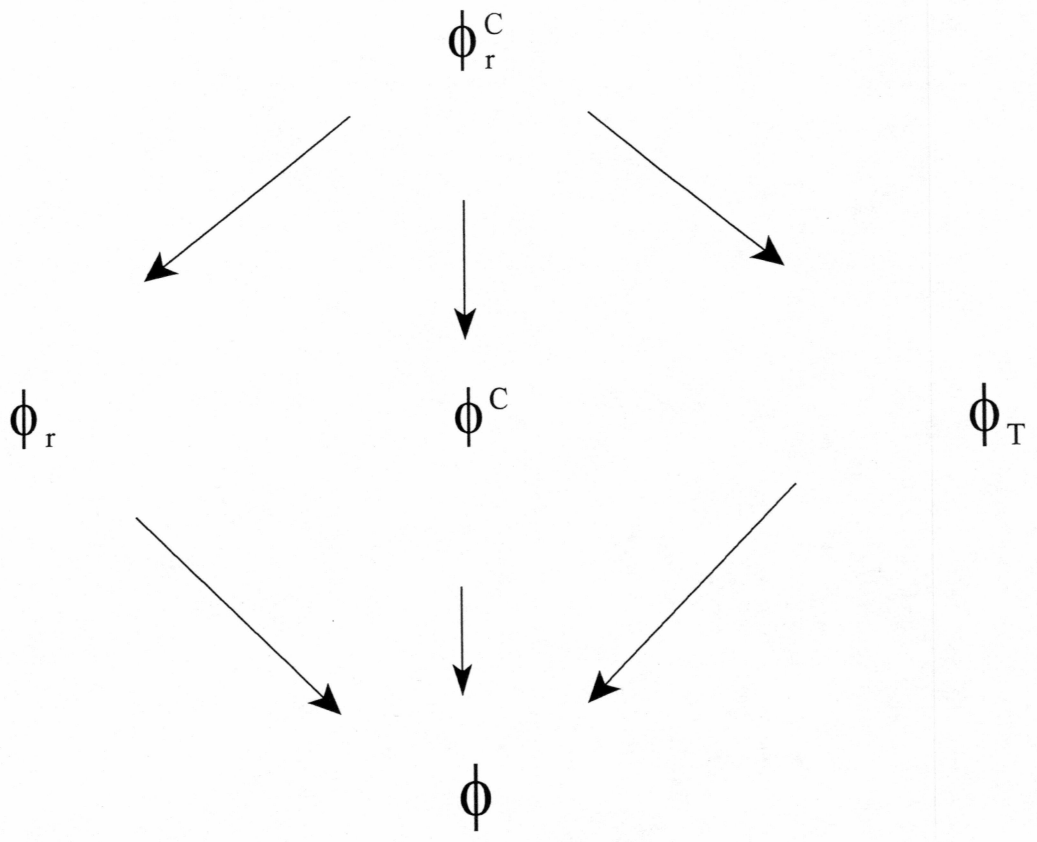

Figure 1.3. Hierarchical model diagram depicting *Clethrionomys rutilus* survival rate (ϕ) structures for models run separately by year under the robust design. Scripts define the type of variation: C = primary trapping period, r = replicate, T = treatment. The arrows indicate decreasing levels of complexity and nested relationships between models.

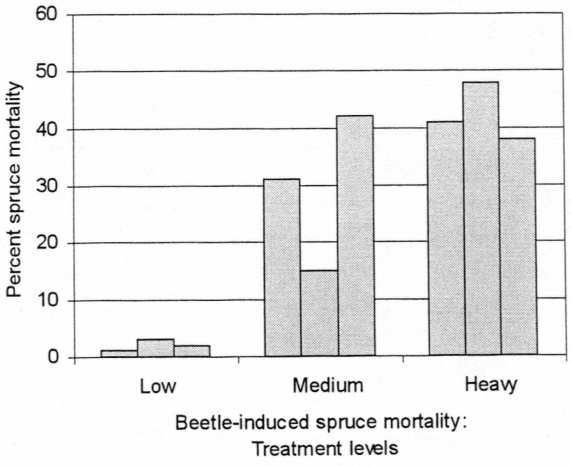

Figure 1.4. Percent beetle-killed spruce on 3 treatment areas. Each treatment area shows spruce mortality levels for 3 replicates within each treatment.

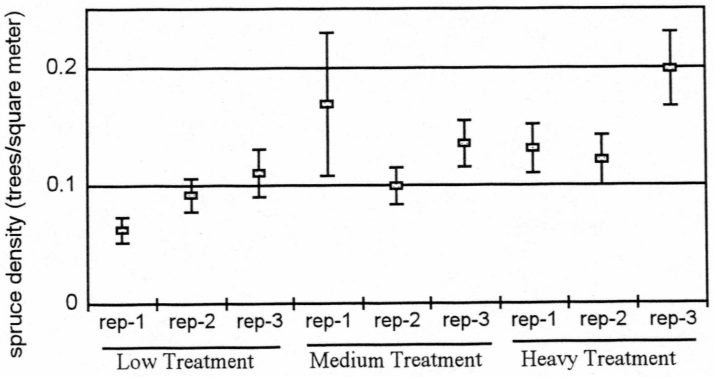

Figure 1.5. Spruce density estimates for 3 treatment areas that have different levels of beetle-induced spruce mortality (low, medium, and heavy). Estimates are shown for 3 replicates within each treatment area. 95% confidence intervals are shown.

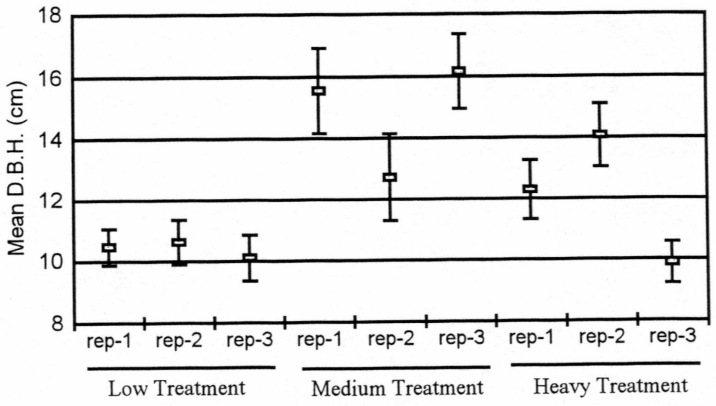

Figure 1.6. Average spruce diameter-at-breast-height for 3 treatment areas that have different levels of beetle-induced spruce mortality (low, medium, and heavy). Averages are shown for 3 replicates within each treatment area. 95% confidence intervals are shown.

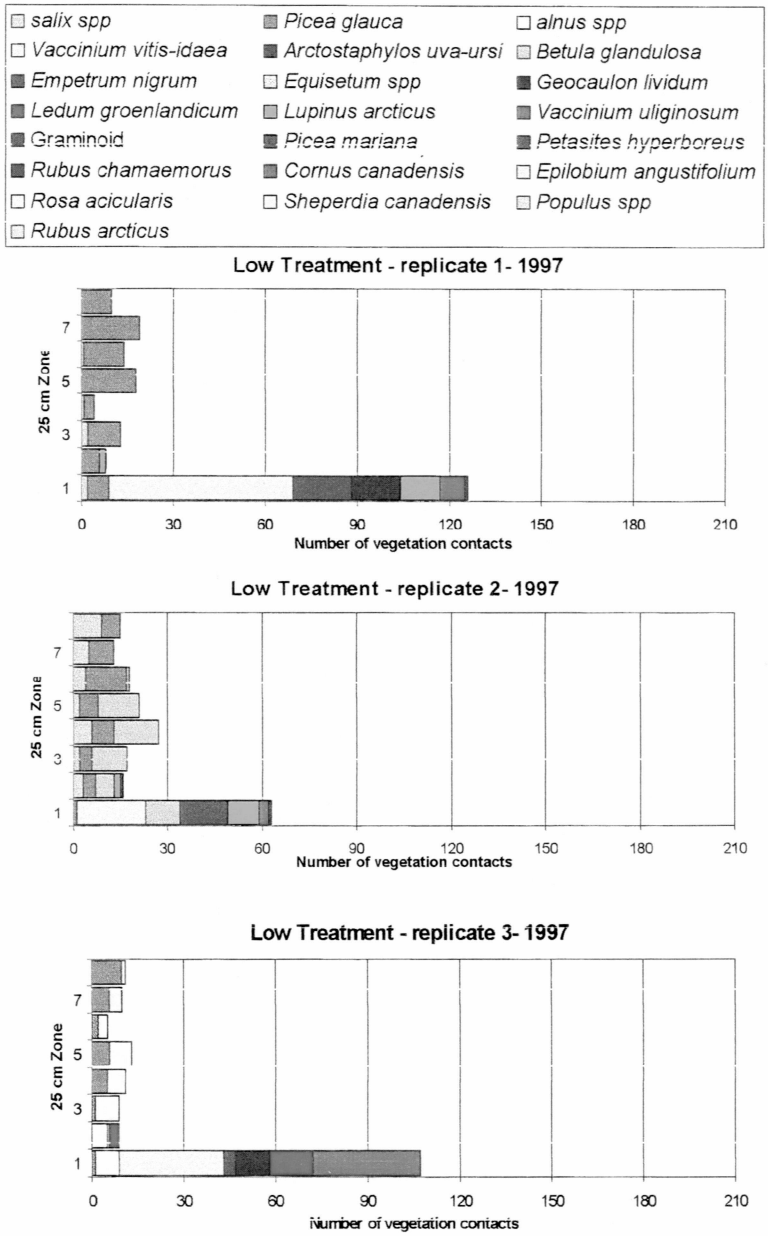

Figure 1.7. Understory vegetation cover for low infestation treatment areas in 1997 as assessed by 2, 50m transect lines using the point-intercept technique. Cover values reflect the average number of vegetation contacts in 25 cm increments (zones) on a vertical rod from ground level to 2m. Samples were taken every meter. Treatments are defined as low, medium, or heavy according to degree of beetle-induced spruce mortality.

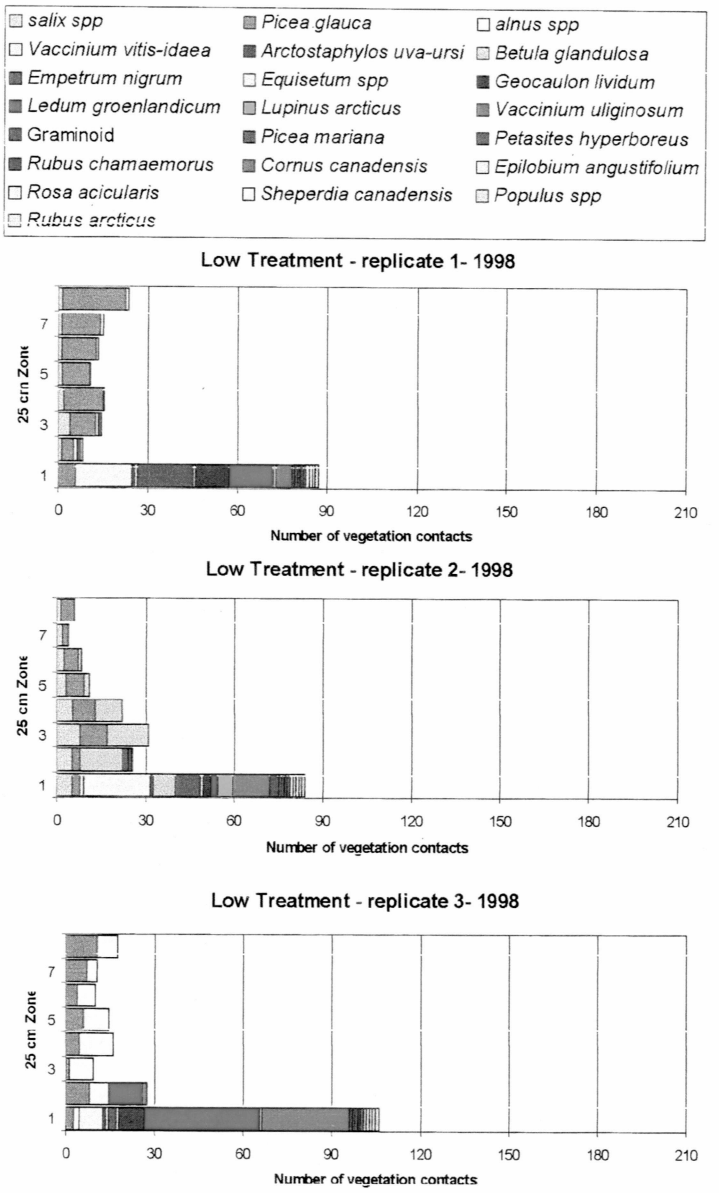

Figure 1.8. Understory vegetation cover for low infestation treatment areas in 1998 as assessed by 2, 50m transect lines using the point-intercept technique. Cover values reflect the average number of vegetation contacts in 25 cm increments (zones) on a vertical rod from ground level to 2m. Samples were taken every meter. Treatments are defined as low, medium, or heavy according to degree of beetle-induced spruce mortality.

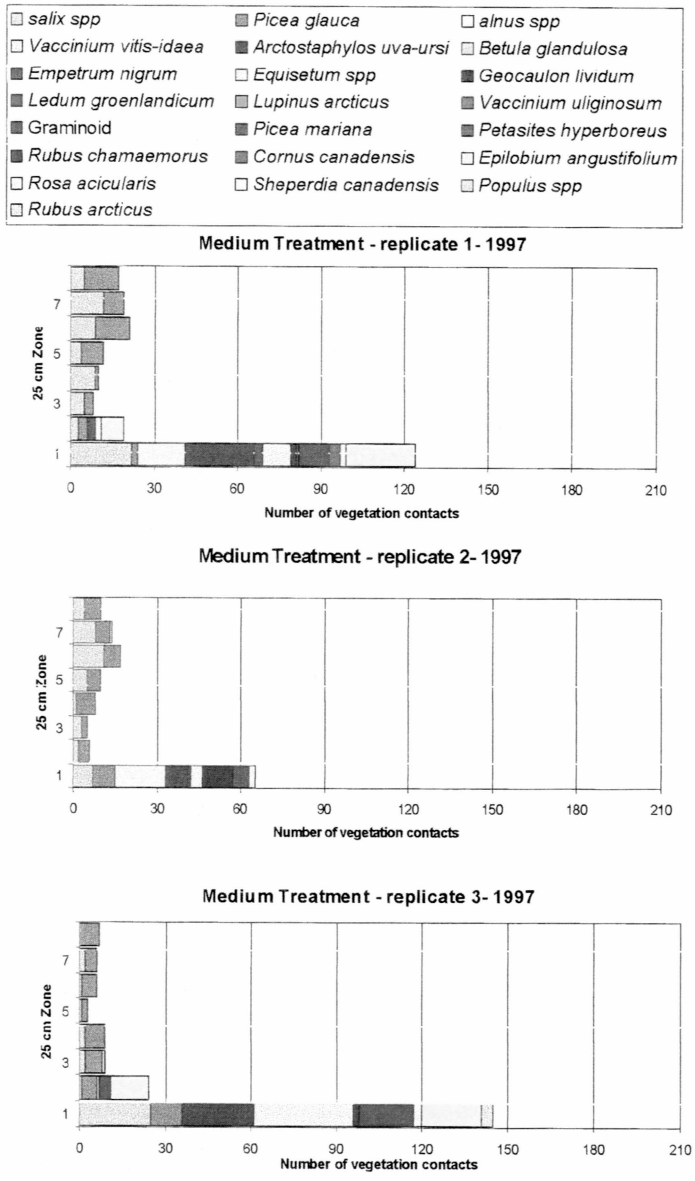

Figure 1.9. Understory vegetation cover for medium infestation treatment areas in 1997 as assessed by 2, 50m transect lines using the point-intercept technique. Cover values reflect the average number of vegetation contacts in 25 cm increments (zones) on a vertical rod from ground level to 2m. Samples were taken every meter. Treatments are defined as low, medium, or heavy according to degree of beetle-induced spruce mortality.

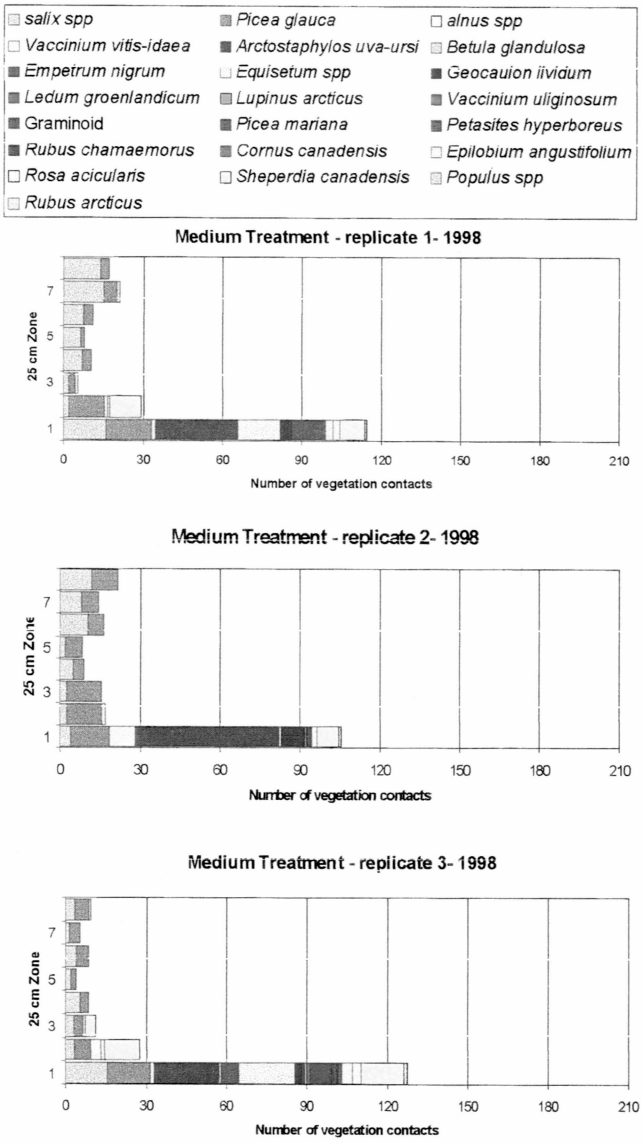

Figure 1.10. Understory vegetation cover for medium infestation treatment areas in 1998 as assessed by 2, 50m transect lines using the point-intercept technique. Cover values reflect the average number of vegetation contacts in 25 cm increments (zones) on a vertical rod from ground level to 2m. Samples were taken every meter. Treatments are defined as low, medium, or heavy according to degree of beetle-induced spruce mortality.

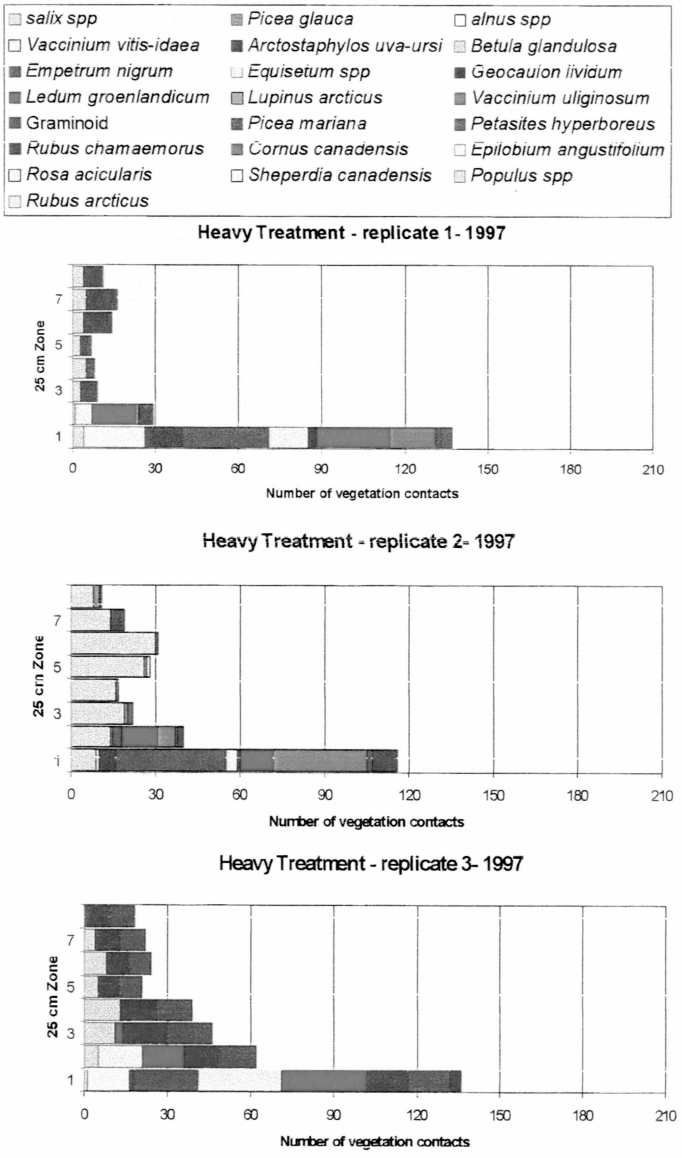

Figure 1.11. Understory vegetation cover for heavy infestation treatment areas in 1997 as assessed by 2, 50m transect lines using the point-intercept technique. Cover values reflect the average number of vegetation contacts in 25 cm increments (zones) on a vertical rod from ground level to 2m. Samples were taken every meter. Treatments are defined as low, medium, or heavy according to degree of beetle-induced spruce mortality.

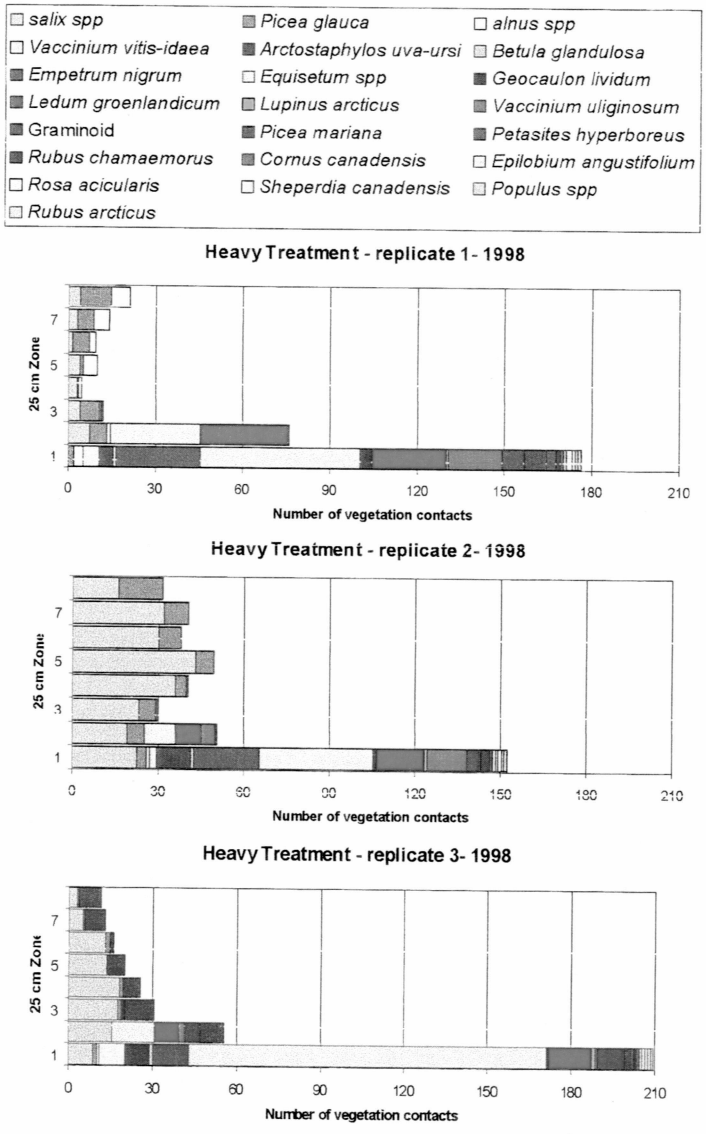

Figure 1.12. Understory vegetation cover for heavy infestation treatment areas in 1998 as assessed by 2, 50m transect lines using the point-intercept technique. Cover values reflect the average number of vegetation contacts in 25 cm increments (zones) on a vertical rod from ground level to 2m. Samples were taken every meter. Treatments are defined as low, medium, or heavy according to degree of beetle-induced spruce mortality.

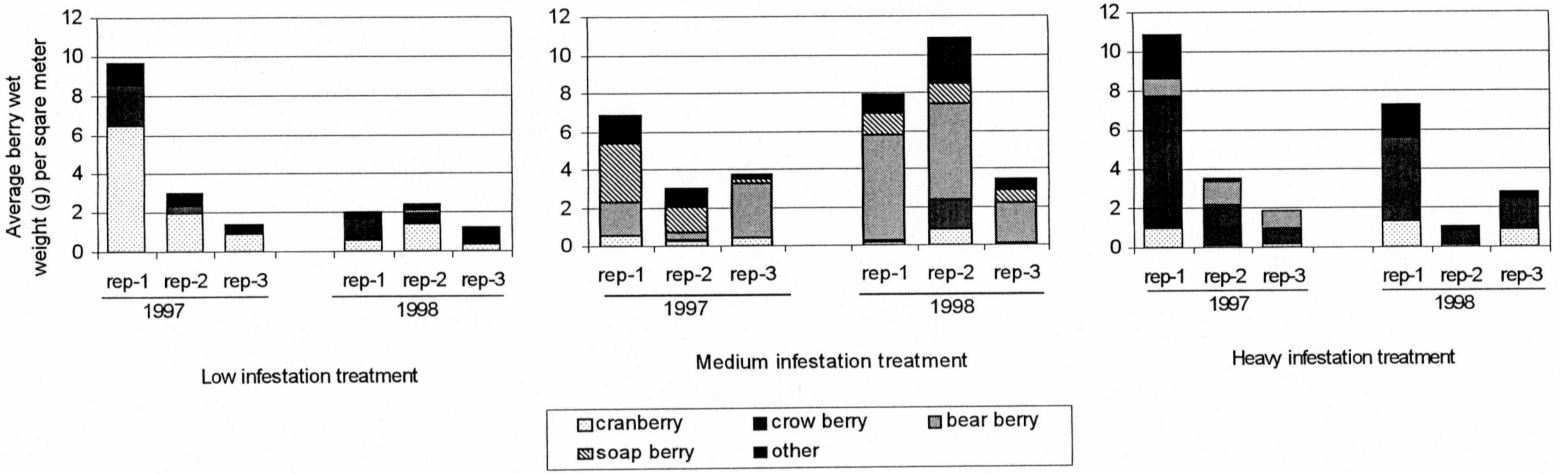

Figure 1.13. Sampled berry availability on 3 treatment areas defined by the level of beetle-induced spruce mortality (low, medium, and heavy). Each graph shows average wet-weight/m^2 for samples collected in 1997 and 1998 on 3 replicate grids within each treatment area. Berries are separated by species.

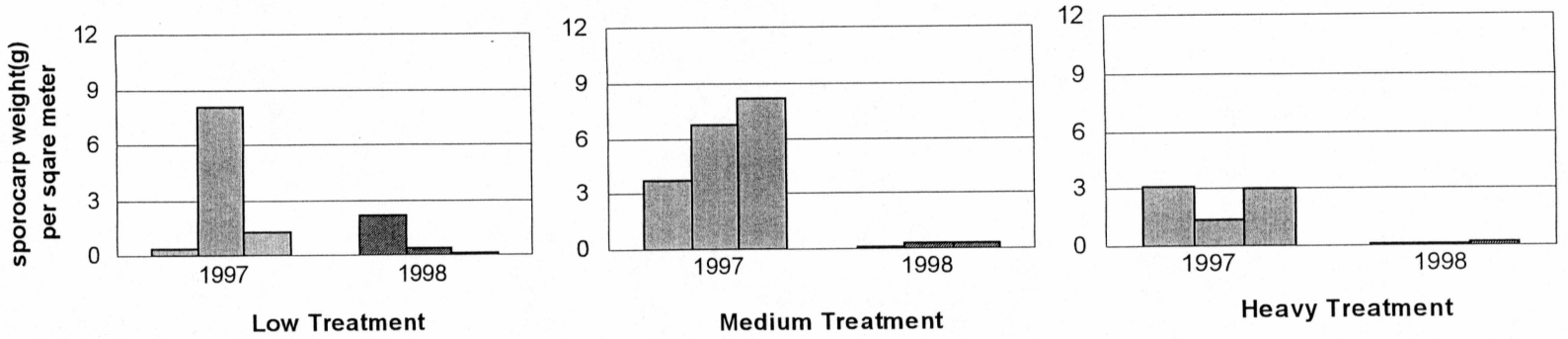

Figure 1.14. Sampled sporocarp availability on 3 treatment areas defined by the level of beetle-induced spruce mortality (low, medium, and heavy). Each graph shows average wet-weight per meter^2 for samples collected in 1997 and 1998 on 3 replicate grids within each treatment area.

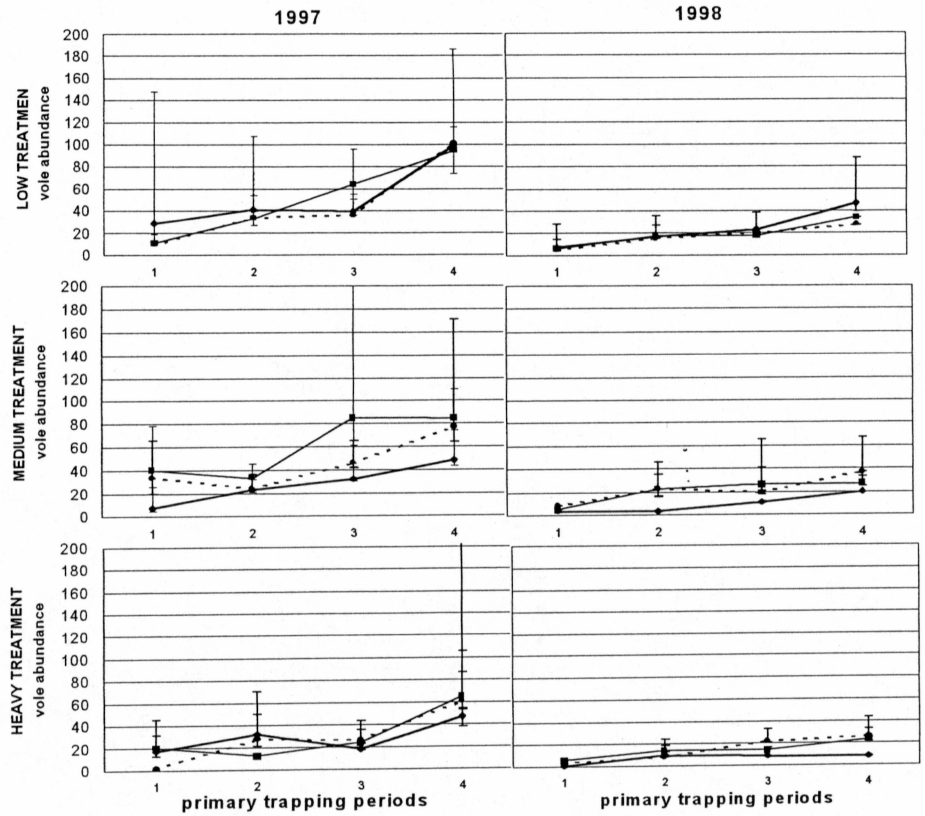

Figure 1.15. Abundance estimates for *Clethrionomys rutilus* populations in 3 white spruce forested areas in the Copper Basin, AK that vary in degree of beetle-induced spruce mortality (treatments = low, medium, and heavy). Abundance estimates for 3 replicates within each treatment are depicted on each graph. 95% confidence intervals are shown. Primary trapping periods occurred approximately every three weeks starting in late May or early June and ending in late August or early September.

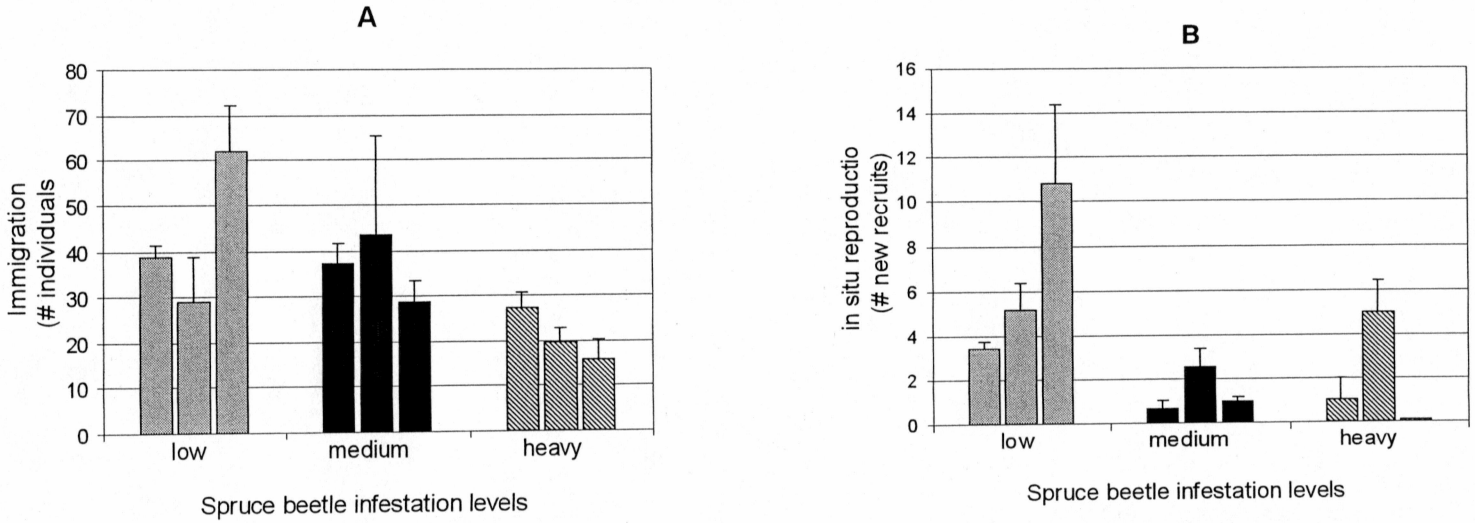

Figure 1.16. Estimates of recruitment for *Clethrionomys rutilus* populations partitioned into components of immigration (A) and in situ reproduction (B). Estimates are produced from 3 white spruce locations in the Copper Basin, Alaska that have different levels of spruce beetle infestations (low, medium, and heavy). Each area has 3 recruitment estimates for each of 3 replicate grids. Note the scale difference between the charts.

Table 1.1. Percentage of individual closed models selected in program CAPTURE for *Clethrionomys rutilus* abundance estimates separated by sex. Model subscripts define sources of capture probability variation: o = no variation, h = individual heterogeneity, b = behavioral response, t = temporal response. Number of estimates for each sex and each year are given in parentheses.

Models selected	Males		Females	
	1997(35)	1998(35)	1997(34)	1998(32)
M_o	6	23	9	19
M_h	49	11	35	25
M_b	20	23	12	3
M_{th}	9	23	18	38
M_{tb}	6	6	9	0
M_{bh}	11	14	18	16

Table 1.2. Model description and selection results under the robust design for variation in *Clethrionomys rutilus* capture(p)/recapture(c) probabilities in 1997 and 1998 data analyzed separately. Data for males and females in each year are pooled. The lowest AIC indicates the most parsimonious model. Survival rate structure with variation across replicates and primary periods was maintained. Emigration/immigration parameters were set to 0. Number of parameters may differ for the same model structure between years due to a different additive time and behavioral effect modeled between capture and recapture probabilities uniquely each year.

Model	1997		1998		Biological description of modeled variation in capture/recapture probabilities
	# parameters	AIC	# parameters	AIC	
p_T^C , c_T^C	**88**	**2275.2**	**79**	**1584.7**	**Variation between treatments and primary trapping periods**
p_r^C , c_r^C	136	2311.0	112	1610.7	Variation between replicates and primary trapping periods
p^C , c^C	72	2396.3	72	1716.5	Variation between primary trapping periods
p_T , c_T	70	2426.5	70	1725.8	Variation between treatments
p , c	66	2425.6	66	1718.3	No variation
p_r , c_r	82	2424.5	82	1737.6	Variation between replicates
$p^C_{r \times sp}$, $c^C_{r \times sp}$	256	2311.0	280	1788.9	Variation between secondary trapping periods, and primary trapping periods

Table 1.3. Model description and selection results under the robust design for *Clethrionomys rutilus* survival rates in 1997 and 1998 data analyzed separately. The modeled capture/recapture probability structure maintained variation between treatments and primary trapping periods. Emigration/immigration parameters were set to 0. Data for males and females in each year were pooled. The lowest AIC indicates the most parsimonious model.

Model	# parameters	1997 AIC	1998 AIC	Biological description of variation in survival rates
ϕ^{C}	**64**	**2255.2**	**1156.3**	**Variation between primary periods**
ϕ_{T}	64	2275.5	1569.3	Variation between treatments
ϕ_{r}	70	2276.8	1579.2	Variation between replicates
ϕ_{r}^{C}	88	2275.2	1584.7	Variation between replicates and primary periods
ϕ	62	2276.9	1565.4	No variation

Table 1.4. Model description and selection results for *Clethrionomys rutilus* survival rates for years 1997 and 1998 combined where survival rates varied in each year by primary trapping period (φ^c). The modeled capture/recapture probability structure maintained variation between treatments and primary trapping periods. Emigration/immigration parameters were set to 0. Data for males and females were pooled. The lowest AIC indicates the most parsimonious model.

Model	# parameters	AIC	Biological description of modeled variation in survival rates
$\phi^{C \times 97trend}$	**126**	**3818.5**	**Interaction between primary period and year where 1997 survival was modeled with a linear trend**
$\phi^{C \times Y}$	127	3820.5	Interaction between primary period and year
ϕ^{C}	124	3829.9	Constant between years
$\phi^{C + Y}$	125	3831.2	Additive relationship between primary period and year

Table 1.5. Results of *Clethrionomys rutilus* survivorship model AIC values using habitat variables measured on each replicate as group covariates. Group covariates were added to the model where survival structure showed an interaction between primary period and year, and 1997 survival was modeled with a positive linear trend. The modeled capture/recapture probability structure maintained variation between treatments and primary trapping periods. Emigration/immigration parameters were set to 0. Data for males and females were pooled. The lowest AIC indicates the most parsimonious model.

Model	# parameters	AIC	Biological description of added covariate
$\phi^{C \times 97 trend}_{spruce\ density}$	**127**	**3817.0**	**Spruce density**
$\phi^{C \times 97 trend}$	126	3818.5	No covariate added
$\phi^{C \times 97 trend}_{\%beetle\ -\ kill}$	127	3819.7	Percent beetle-killed spruce
$\phi^{C \times 97 trend}_{sporocarps}$	127	3820.1	Vole food (epigeous sporocarps availability)
$\phi^{C \times 97 trend}_{vegetation\ cover}$	127	3820.5	Understory vegetation cover
$\phi^{C \times 97 trend}_{berries}$	127	3820.6	Vole food (berry availability)

Table 1.6. *Clethrionomys rutilus* 30-day survival rate (φ) estimates across 3 primary trapping periods for 1997 and 1998. Data for males and females are pooled. The level of beetle-induced spruce mortality defines each treatment as low, medium, and heavy. Each treatment contains 3 replicate 1ha grids. Estimates are produced from model averaging where the % variation associated with model uncertainty is shown for each replicate φ estimate.

	φ^{1st} (SE)	% variation due to model uncertainty	φ^{2nd} (SE)	% variation due to model uncertainty	φ^{3rd} (SE)	% variation due to model uncertainty
1997						
Low treatment						
Replicate 1	.18 (.038)	10.0	.29 (.031)	30.4	.43 (.038)	31.9
Replicate 2	.20 (.040)	6.0	.32 (.030)	9.4	.47 (.034)	6.1
Replicate 3	.19 (.039)	4.4	.30 (.030)	11.9	.45 (.036)	13.4
Medium treatment						
Replicate 1	*0 (0.0)	0	.34 (.037)	36.3	.48 (.041)	33.5
Replicate 2	.21 (.042)	7.9	.33 (.032)	13.6	.47 (.036)	10.5
Replicate 3	.20 (.040)	4.4	.32 (.030)	7.8	.46 (.035)	5.7
Heavy treatment						
Replicate 1	.19 (.039)	1.4	.30 (.030)	5.1	.45 (.036)	5.7
Replicate 2	.19 (.039)	3.8	.31 (.029)	8.0	.45 (.036)	6.3
Replicate 3	.17 (.038)	22.0	.28 (.034)	45.6	.42 (.044)	45.8
1998						
Low treatment						
Replicate 1	.61 (.115)	4.8	.22 (.048)	13.7	.45 (.050)	21.6
Replicate 2	.64 (.111)	1.8	.24 (.050)	1.7	.49 (.048)	3.5
Replicate 3	.62 (.113)	1.2	.23 (.048)	3.5	.47 (.048)	4.6
Medium treatment						
Replicate 1	.66 (.109)	6.1	.26 (.054)	12.0	.51 (.052)	21.1
Replicate 2	.64 (.110)	2.4	.25 (.051)	3.3	.49 (.048)	7.1
Replicate 3	.64 (.111)	1.1	.24 (.050)	1.2	.48 (.048)	2.1
Heavy treatment						
Replicate 1	.62 (.113)	1.0	.23 (.049)	2.4	.47 (.048)	3.2
Replicate 2	.63 (.112	1.5	.23 (.049)	2.3	.47 (.048)	3.0
Replicate 3	.59 (.118)	10.5	.21 (.049)	25.0	.44 (.054)	36.4

* Grid location changed after first trapping period, therefore, φ could not be estimated

Chapter 2*. Movement distances of northern red-backed voles (*Clethrionomys rutilus*) in response to varying demographic characteristics and habitat quality.

ABSTRACT

Theory on microtine mating systems predicts that male spacing behavior will be related to the availability of females, whereas female spacing is determined by the quality of the habitat. Movements of individual red-backed voles (*Clethrionomys rutilus*) were studied through intensive live-trapping during the snow free seasons of 1997 and 1998 in the Copper River Basin, Alaska. Movement distances were assessed by measuring the average distance moved between successive captures (ADM) within 5-day livetrapping periods. In a sample of 337 female and 585 male voles, ADM for males (23.8 m, SE = 0.2 m) was significantly greater than females (15.6 m, SE = 0.2 m) ($t = 10.7$, d.f. = 906, $P < 0.001$). Male ADM was negatively associated with an increase in female-biased sex ratios and possibly related to food availability. Female movement distances were not related to population density, but greater food availability appeared to be interacting with other factors to decrease female ADM. Female juvenile/subadult age classes had much larger ADM than adult females. Our data suggests that male vole movement distances were influenced by female availability while females appeared to be responding to food resources (epigeous sporocarps).

* Prepared for submission in the Journal of Mammalogy

INTRODUCTION

Movement patterns are an integral component contributing to the demographic processes of animal populations. Factors both extrinsic and intrinsic to the population can influence movement patterns. For small mammal populations, potential extrinsic influences include habitat fragmentation (Diffendorfer et al. 1995, Peles et al. 1999), food availability (Taitt et al. 1981, Ostfeld 1986, Ims 1987), predation (Erlinge et al. 1983, Anderson 1986), weather (Vickery and Bider 1981), and season (Erlinge et al. 1990, Rodgers 1990, Salvioni and Lidicker 1995). Possible intrinsic factors include dominance relationships of individuals (Nelson 1995), competition (Bond and Wolff 1999), genetic relatedness of individuals (Hestbeck 1982, Hestbeck 1988, Ims 1989, Ishibashi et al. 1997), and population size (Ostfeld 1986, Erlinge et al. 1990, Nelson 1995a, Agrell et al. 1996). Agrell et al. (1996) emphasized that multiple variables need to be considered when attempting to create predictive models for determining microtine spatial patterns. We measured movement distances for northern red-backed vole (*Clethrionomys rutilus*) individuals and used demographic characteristics and habitat variables from different populations to explore factors influencing movement distances.

In the genus *Clethrionomys*, males tend to have overlapping home ranges that are much larger than female home ranges (Bondrup-Nielsen and Karlsson 1985). Most species within the genus *Clethrionomys* are thought to display polygyny, where male home ranges overlap and are hypothesized to be determined by the density and distribution of females. Female home ranges are usually exclusive and believed to be determined by the quality of the habitat (i.e., abundance of food resources) (for review see Bondrup-Nielsen and Karlsson 1985).

Population density effects on home range size and social structure can influence population dynamics (Erlinge 1990), but evidence from microtines is often conflicting. Fluctuations in population density do not appear to influence female home range size (Bondrup-Nielson 1986, Sandell et al. 1990, but see Fortier and Tamarin 1998), whereas

male home ranges are often inversely related to population density (Mazurkiewicz 1981, but see Fortier and Tamarin 1998). Male voles have been found to decrease their movements in response to increased female density (Nelson 1995b), increased female-biased sex ratio (Sandell et al. 1991), and increased male density (Bond and Wolff 1999). Female home range size has been found to decrease with improved habitat quality and/or food addition (Mazurkiewicz 1971, Viitala 1977, Ims 1987). Vole movements have been found to increase as the amount of protective vegetation cover increased (Taitt et al. 1981). There is considerable variation in vole space use across species within the genus *Clethrionomys* (Viitala 1977, Viitala and Pusenium 1990). Voles have extremely flexible social behavior (Agrell et al. 1996), and different habitats and/or population dynamics may induce intraspecific variation in movement patterns.

Various home range measurements are often employed to determine microtine space use (Batzli and Henttonen 1993). Live-trapping has been found to give adequate home range assessments if individuals are captured on at least 8 occasions (Desy et al. 1989). When comparing movements between different populations, a measure of the distance moved may be sufficient, rather than an area measurement (Slade and Russell 1998). We used the average distance moved between successive captures (ADM) to assess red-backed vole movements. ADM has been found to be highly correlated with home range measurements (Slade and Russell 1998) and has the advantage of utilizing information from individuals captured infrequently.

As part of an assessment of the impact of spruce bark beetle (*Dendroctonus rufipennis*) infestations on microtine populations in the Copper River Basin, our analysis was designed to measure movement distances and determine demographic and/or habitat related variables that influenced the movements of male and female red-backed voles. We live-trapped in 9 populations of voles on plots that had differing levels of spruce mortality due to bark beetle infestations, and variable demographic and habitat characteristics. Males were hypothesized to move greater distances than females. Male

movements have historically been thought to respond to female availability (Ostfeld 1985), and more recently, to competition from other males (Bond and Wolff 1999). We hypothesized that if males are responding to female availability, male movement distances would decrease in response to greater female biased sex ratios and greater number of females in the population. On the other hand, if male-male competition affected male movement distances, male ADM should decrease when the sex ratio is biased towards males (Bond and Wolff 1999). Female movements are thought to be habitat quality related (Mazurkiewicz 1971, Viitala 1977, Ims 1987). Female ADM was predicted to be inversely related to food availability (berries and epigeous sporocarps), and to decrease at lower levels of vegetation cover. The movement response of red-backed voles to different levels of beetle infestation was evaluated to add to our understanding of how infestations affect space use by voles.

METHODS

Study area

The study was conducted along a 35 km stretch of the Richardson Highway 40 km south of Glennallen in the Copper River Basin (61° N, 145° W), south-central Alaska, USA. Winters extend over 6 months and the average monthly temperatures range from a high of 13.4 °C in July to -21.0 °C in January. Average annual rainfall was 30 cm and average snow depths reach 165 cm. The vegetation community, as described in Gallant et al. (1995), was dominated by white spruce (*Picea glauca*) and black spruce (*P. mariana*) forests underlain by *Salix* and *Alnus* spp.; a short shrub layer of *Shepherdia canadensis, Ledum groenlandicum, Betula glandulosa, Vaccinium uliginosum*; a ground layer of *Geocaulon lividum, V. vitis-idaea, Empetrum nigrum, Arctostaphylos uva-ursi,* and moss (*Sphagnum* spp.). Study areas, consisting of 9, 1-ha grids, were selected in white spruce forests with levels of beetle-induced spruce mortality ranging from 1-48 %.

Habitat quality

The point-centered-quarter (PCQ) method, employed to measure spruce density, was also used to measure percent beetle-killed spruce on each grid (Higgins et al. 1996). On 50 randomly selected points on each replicate grid, the distance to the nearest spruce tree within 4 quadrants around the point was measured while beetle damage on each tree was assessed. The understory vegetation was measured using 2, 50 m transect lines employing the point-intercept technique to assess vegetation vertically on a sampling rod from ground level to a height of 2 m, at 1 m intervals (Higgins et al. 1996). Vegetation cover is indexed by the mean number of times the sampling rod intercepts a plant part during vertical placement. *C. rutilus* food resources were assessed on each study replicate by counting and weighing (wet-weight) epigeous sporocarps and berries (*Vaccinium uliginosum*, *V. vitis-idaea*, *Rosa acicularis*, *Geocaulon lividum*, *Arctostaphylos uva-ursi*, *Empetrum nigrum*, *Rubus chamaemorus*, *Rubus arcticus*, and *Shepherdia canadensis*) in 50 randomly selected 1 m^2 quadrats on each replicate (Johnson et al. 1995). This assessment, as well as PCQ and understory vegetation cover evaluations, was conducted at the beginning of August in 1997 and 1998 to coincide with the peak of berry and sporocarp development.

We interpreted habitat quality to be based on food availability (berries and sporocarps) and protective understory vegetation cover. Beetle-induced spruce mortality may affect vole habitat quality by influencing food resources, predation pressure, or other factors. We used beetle infestation level as another possible measure of habitat quality. Measures of habitat characteristics were inserted as independent variables in ANOVA models assessing their influence on vole movement distances (see **Movement** section below).

Trapping procedures

Live trapping occurred on 9, 1 ha grids which were arranged in an 11 x 11 array of trapping stations with 10 m intervals. A single Sherman live-trap (23x8x9 cm) was placed

at each of the 121 stations. Traps were open for 5 days and checked 3 times daily except day 5 when the traps were checked and closed in the morning. Traps were set with sunflower seeds and cotton bedding material, and restocked after each capture. Captured voles were individually marked with a passive integrated transponder (PIT) tag (Schooley et al. 1993). Weight, capture location, and standard external reproductive data (males: testes scrotal or abdominal, females: pregnant, lactating, and vulva open or closed) were noted for each capture. Each grid was subjected to 4 trapping sessions separated by 16-30 day intervals throughout the snow-free periods of 1997 and 1998 beginning in late May-early June and ending in late August-early September.

Abundance

Abundance was assessed using the number of individual voles caught on each grid during each trapping session. *A priori* knowledge of homogeneity in vole capture probabilities on our grids provided a rational for using the number of individual voles caught (catch indices) rather than abundance estimates (Skalski and Robson 1992:121). The number of voles caught fluctuated across the trapping periods and years (2-89 individuals per grid).

Movement

C. rutilus capture data were transformed into capture histories (e.g., Otis et al. 1978) displaying when each individual was captured and the corresponding grid coordinate of each capture. Capture histories were read in program CAPTURE (Otis et al. 1978, Rexstad and Burnham 1992) to generate the average distance moved between successive captures (ADM and a SE) for *C. rutilus* individuals.

Female voles were separated into age classes based on weight. Individuals < 20 g were classified as subadults/juveniles and individuals > 20 g were classified as adults based on signs of reproductive maturity. Non-reproductive females often remain on their natal home range and thus, were captured frequently. Non-reproductive males (testes abdominal) were captured infrequently, most likely due to high dispersal rates. Therefore, males were not subject to age specific categorization.

Based on sex-specific space use differences outlined by Bondrup-Nielsen and Karlsson (1985), we chose to assess factors influencing movement separately by sex. To confirm sex-specific movement distances, we preformed a *t*-test comparing male and female ADM. We assessed the movement response of each sex to vole abundance, age (females), sex ratio, understory vegetation cover, berry and *sporocarp* availability, and percent beetle-killed spruce using a 6-way (7-way for females) ANOVA using PROC GLM in SAS (SAS Institute Inc. 1996). To discount individuals whose movement distance is poorly estimated, the movement response (ADM) was weighted by [variance (ADM) $^{-1/2}$]. Significance of main effects and all 2-way interactions were analyzed using type III sum of squares. Interactions greater than 2-way were not included in the models.

Independent variables (vole abundance, sex ratio, and habitat quality measures) were categorized before their influence on ADM was assessed. Category distinctions were set to have sample sizes equivalent across categories. Category definitions and sex specific sample sizes for each category are shown for each independent variable (Figure 2.1A-G).

RESULTS

Nine hundred and twenty-two red-backed voles (585 males and 337 females) were captured at least 3 times during 5-day sampling sessions. The mean number of captures per individual was 7.0 (SE = 0.1). The mean number of captures between the sexes was similar (males: 6.9, SE = 0.1, females: 7.1, SE = 0.2). ADM for males (23.8 m, SE = 0.2 m) was significantly greater than for females (15.6 m, SE = 0.2 m) (t = 10.7, d.f. = 906, P < 0.001) (Figure 2.2).

The ANOVA model assessing male movement distances was significant (F = 7.56, d.f. = 49, P < 0.001, R^2 = 0.41). Sex ratio and level of beetle-killed spruce were

significant variables influencing male ADM along with several interactions (Table 2.1). Male ADM decreased when female biased sex ratio increased (Figure 2.3). Male ADM did not vary greatly in low versus high beetle-killed spruce forests (low = 19.4 m, SE = 0.2 m; high = 19.8 m, SE = 0.2 m). The male movement response to the interaction between abundance and sex ratio was variable (Figure 2.4). Interactions between sex ratio and sporocarp availability (Figure 2.5) and berry availability (Figure 2.6) show large variations across food availability levels in all sex ratio categories except at the highest female biased sex ratio category. The interaction between vole abundance and sporocarp availability showed a general tendency for ADM to decrease as sporocarp availability increased, except when abundance was at intermediate levels (Figure 2.7).

The ANOVA model assessing female ADM was significant ($F = 3.15$, d.f. = 63, $P < 0.001$, $R^2 = 0.42$) (Table 2.2). Individuals were infrequently categorized in both age classes (< 6%). Female juvenile/subadult ADM was larger than adult ADM (Figure 2.8). This effect was also shown in a significant interaction between beetle-induced spruce mortality level and age (Figure 2.9). Although sex ratio had a significant effect on female ADM, there was not large variation between the sex ratio categories (Figure 2.10). The significant interaction between sporocarp availability and beetle-induced spruce mortality showed female ADM generally decreased with increasing sporocarp availability (Figure 2.11). The interaction between vole abundance and berry availability did not display any clear pattern (Figure 2.12).

DISCUSSION

To maximize fitness in polygynous mating systems, females should maximize offspring survival, whereas males should mate with as many females as possible (Trivers 1972). These strategies result in differential use of space and movement patterns between the sexes. For microtine populations, these differences are shown with males consistently having much larger home ranges than females (for review see Bondrup-Nielsen and

Karlsson 1985). Our data show greater movement distances in males than females (Figure 2.2), and further address questions of which resources are driving these movement differences in northern red-backed voles.

If male movement distances are determined by female availability, we would expect male ADM to decrease as more females enter the population. As female density increased, males could gain access to an equal or greater number of females while minimizing the costs associated with traversing and defending larger territories (Bond and Wolff 1999). We were unable to find a significant effect of total vole abundance on male ADM (Table 2.1). Lack of significance in male ADM response to population size does not support previous studies showing male movements decreasing with greater population density (Gurnell and Gipps 1989, Nelson 1995b). However, male movements showed a varied response to abundance in different sex ratio categories (Figure 2.4). In the sex ratio category that had the largest proportion of females per male, male ADM decreased as abundance increased (Figure 2.4). This suggests that males may not be responding to factors associated with high population densities, such as intrasexual competition or number of available females, until there is a large proportion of females to males in the population.

Population density may not be an adequate variable from which to assess male movements because male response to increasing female density cannot be isolated from increased male-male competition due to a concomitant increase in male density. Increasing the female population through manipulation could overcome male competition effects (see Nelson 1995b, Bond and Wolff 1999). Because we did not conduct a manipulation, using sex ratio instead of female population size overcomes implications of competition between males. Sex ratio was significant in our model, and as predicted, male ADM decreased as there were more females per male in the population (Figure 2.3). Similar results were found in populations of *Microtus agrestis* (Sandell et al. 1991). Contracted male movement distances in response to a greater number of females per male

in the population supports the contention that males are responding to the availability of reproductive females in the population (Trivers 1972, Ostfeld 1985), which has been shown to have a profound effect on the potential for reproductive success in males (Ims 1988). Indeed, with theoretical models, the variance in male mating success has been shown to increase as the sex ratio becomes female-biased (Ims 1988). The ratio of females to males may be more informative than female density in explaining male movement distances associated with female availability.

If male movement distances were influenced by intrasexual competition, movement distances would vary inversely with the number of male competitors. In species of *Clethrionomys*, the incidence of male-male aggression increases with population density as assessed from bodily scarring (Ims 1987). Intrasexual competition has been demonstrated in other microtine studies using fluctuations in population size and sex ratio as a means of manipulating potential competition (Bond and Wolff 1999). Using natural density fluctuations to assess competition fails to consider influences of greater female availability that can also affect male movements. Sex ratios that become more male biased could be used as a means of showing competition. Competition between males has been implicated when home range size of males decreased as sex ratios became male-biased (Bond and Wolff 1999). In our study, male ADM increased when sex ratios were male-biased (Figure 2.3). Naturally, competition will be a function of the number of males not just the ratio of males in the population. Male movements did decrease when abundance increased and there was a high proportion of females per male in the population (Figure 2.4). This suggests the effects of male-male competition may be important only when there is a high proportion of females in the population.

Male ADM varied in response to significant interactions between sex ratio and sporocarp availability (Figure 2.5) and berry availability (Figure 2.6). In several sex ratio categories, male ADM decreased as food availability (sporocarp and berry) increased, but the response was variable across most sex ratio categories. Variation in ADM was minor

in the 3 sporocarp availability categories when female-biased sex ratios were > 0.4 (Figure 2.5), and this trend was similar for berry availability (Figure 2.6). This suggests that male movements may have been influenced by food availability until the number of females per male increased sufficiently in the population to constitute a defendable resource (Fortier and Tamarin 1998). Response of male ADM to sporocarp availability also varied with vole abundance (Figure 2.7). In the low (< 25 individuals/ha) and high (> 45 individuals/ha) abundance categories, male ADM decreased when sporocarp availability increased (Figure 2.6). This also suggests that male movements may be responding to food resources.

Female home ranges in the genus *Clethrionomys* have been shown to both respond (Salvioni and Lidicker 1995) and not respond (Bondrup-Nielsen 1986, Gurnell and Gipps 1989) to population size. In our data, vole abundance did not significantly affect female ADM (Table 2.2). Age and sex ratio were significant variables in the ANOVA model assessing female ADM (Table 2.2). Juvenile/subadult vole ADM was greater than adult female ADM (Figure 2.8). Non-reproductive female movements are not restricted by litter care, and greater juvenile/subadult ADM may be a reflection of greater dispersal in this age class. Indeed, increased movement distances registered on trapping grids have been argued to correspond with an increase in dispersal (Sandell et al. 1990).

As food availability decreases, foraging costs increase due to greater travel and search times. Greater movement distances also increase an individual's exposure to predation. These costs are particularly important for female microtines that show a 100% increase in energy requirements during pregnancy and lactation (Kaczmarski 1966). Therefore, if female movement patterns are tied to food resources, female ADM should decrease in response to greater food availability. Food availability variables (berries and sporocarps) were not significant in affecting female ADM (Table 2.2). However, despite the significant interaction between sporocarp availability and beetle-induced spruce

mortality, females showed a decrease in ADM from the low to high beetle-induced spruce mortality levels and a decrease in ADM as sporocarp availability increased in each beetle infestation level (Figure 2.11). This suggests that female ADM was food related and decreased as resources increased.

Female ADM showed a varied response to vole abundance in habitats with different levels of berry availability (Figure 2.12). When vole abundance was at moderate levels (25-45/ha), female ADM responded inversely with berry availability as originally predicted, but there was large variation in the low and high vole abundance categories across berry availability levels (Figure 2.12). Our assessments of food availability were conducted at one point in time. Red-backed vole food resources vary during the year and may be particularly limiting in the spring and early summer (West 1982). Sampling various vole food sources across the vole trapping periods would have given greater insight as to how female movements are tied to food resources.

Female ADM decreased for both age classes from the low to high beetle-induced spruce mortality levels (Figure 2.9). This and the response of female ADM to beetle-induced spruce mortality (Figure 2.11) showed a trend for female ADM to be smaller in areas with high beetle infestation levels. If movement distances decrease in higher quality habitats, this implies that beetle infestations may be improving vole habitat. Movement activity may be a more revealing measure in evaluating vole response to beetle-induced habitat disturbance than vole population parameters (McDonough Thesis Chapter 1).

There was not a response in either sex to variation in vegetation cover level (Tables 2.1 and 2.2). Vegetation cover may not have varied across grids sufficiently to be an informative variable.

Spacing and movement patterns are not species-specific attributes, but are conditional systems adapted to current environmental conditions (Agrell et al. 1996). Much of the variation in our ANOVA models was left unexplained (R^2 ranged from 0.41-

0.42). Knowledge of kinship, dominance relationships, weather, and predation pressures would help explain some of this variation, but we believe our models adequately explained factors influencing movement when considering that large individual variation in space use behavior is the predominant pattern for many microtine species (Ims 1989). In this study, we found that the number of females per male is a factor contributing to the movement patterns of male voles, and males may be responding to food availability until female availability increases sufficiently to constitute a defendable resource. Female voles did not respond to population size but appeared to be responding to habitat quality as assessed through food availability (most notably, sporocarps).

The argument that female reproductive success is limited by their ability to acquire nutrients for the high energetic costs of maternal care, and that male reproductive success is limited by access to mates, is not new (Trivers 1972, Ostfeld 1985). However, the extension of this idea, that female movements are determined by food availability and males by female availability, has been difficult to demonstrate empirically for small mammals. Our data support these arguments, but indicate that there are other sources of variation that might be influencing the movements of the different sexes of red-backed voles.

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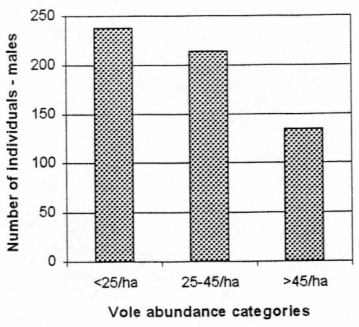

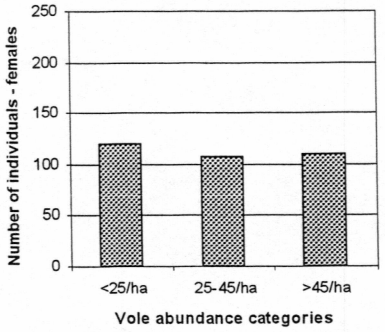

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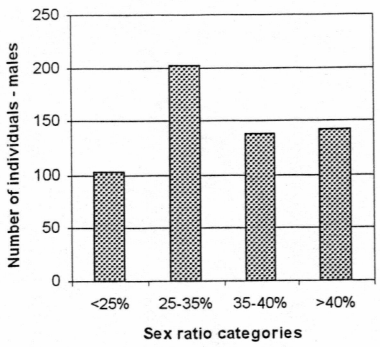

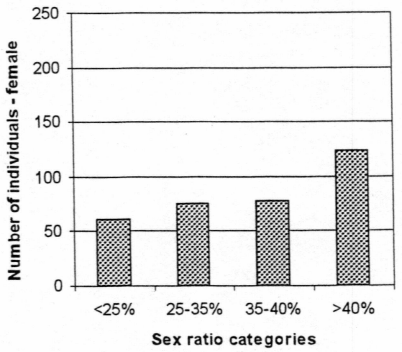

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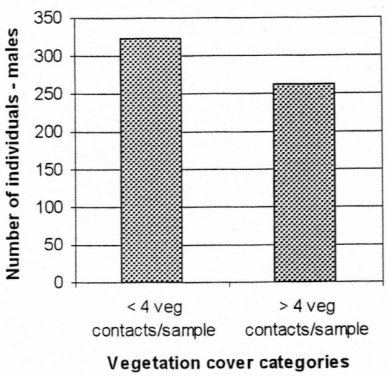


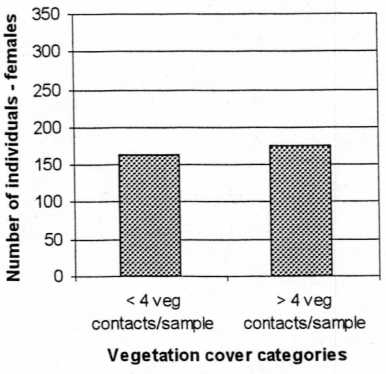
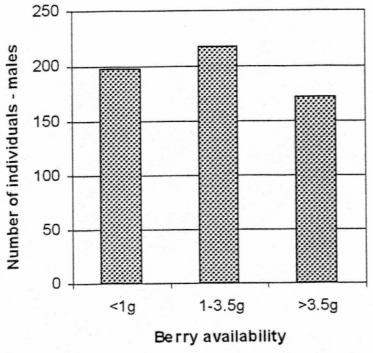
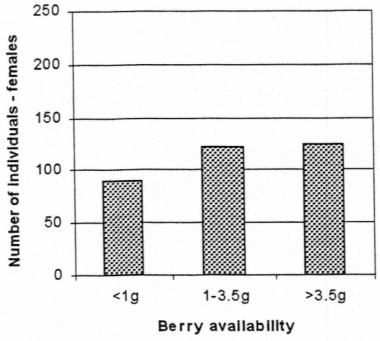


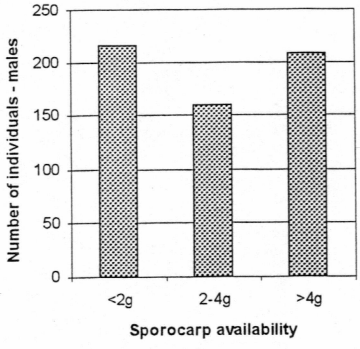
Figure 2.1. Sex specific sample sizes of independent variables used to assess *Clethrionomys rutilus* movement distances. Category descriptions are on the x-axis. The number of individuals in each category is shown on the y-axis. Males and females are graphed separately. Variables include: (A) vole abundance, (B) sex ratio, (C) vegetation cover, (D) berry availability, (E) fungi availability, (F) percent beetle-induced spruce mortality, (G) female age groups.

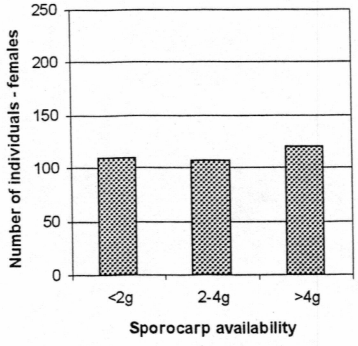
D


Number of individuals - males
250
200
150
100
50
0
<1g
1-3.5g
>3.5g
Berry availability

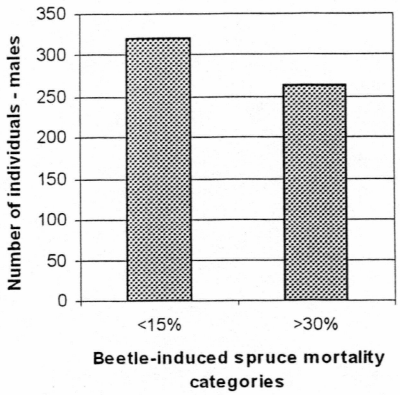

Number of individuals - females
250
200
150
100
50
0
<1g
1-3.5g
>3.5g
Berry availability

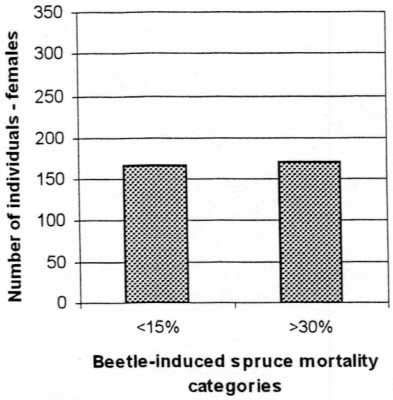
E


Number of individuals - males
250
200
150
100
50
0
<2g
2-4g
>4g
Sporocarp availability

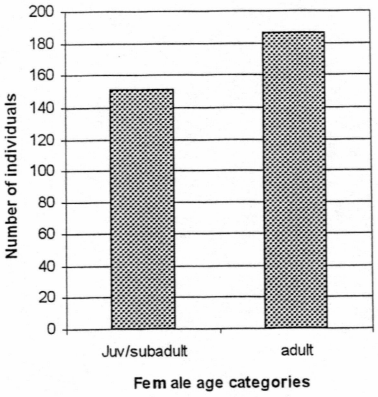

Number of individuals - females
250
200
150
100
50
0
<2g
2-4g
>4g
Sporocarp availability

F


Number of individuals - males
350
300
250
200
150
100
50
0
<15%
>30%
Beetle-induced spruce mortality categories


Number of individuals - females
350
300
250
200
150
100
50
0
<15%
>30%
Beetle-induced spruce mortality categories

G


200
180
160
140
120
100
80
60
40
20
0
Number of individuals
Juv/subadult
adult
Female age categories

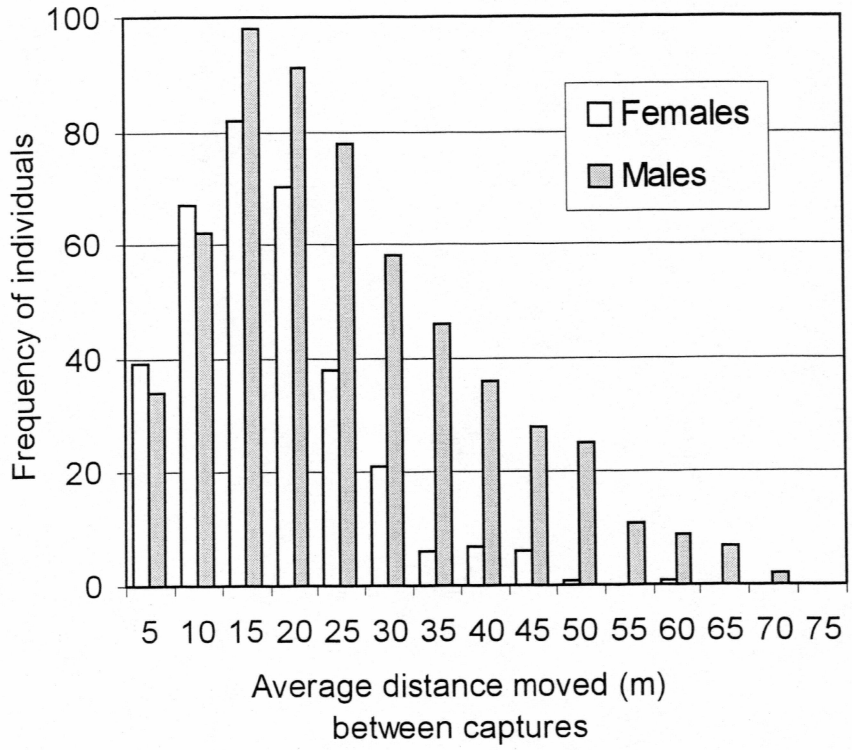


Figure 2.2. Histograms of the average distance moved between successive captures for 585 male and 337 female *Clethrionomys rutilus*. Average distance moved for each individual are shown in 5 meter incremental classes up to 75 meters.

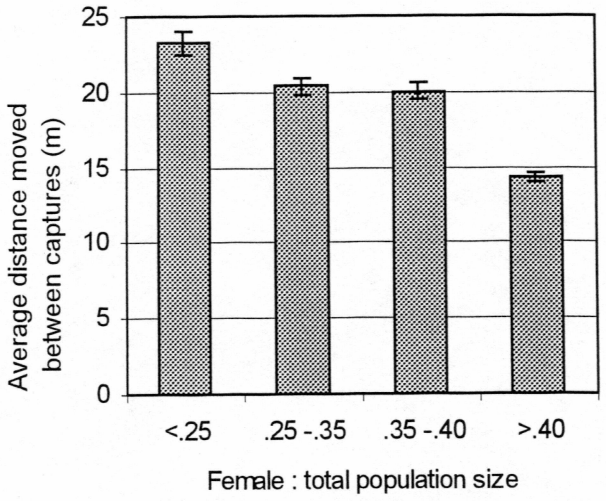


Figure 2.3. Average distance moved in meters between successive captures of 585 male *Clethrionomys rutilus* in response to 4 sex ratio categories (females : total population size). 95% confidence intervals are shown.

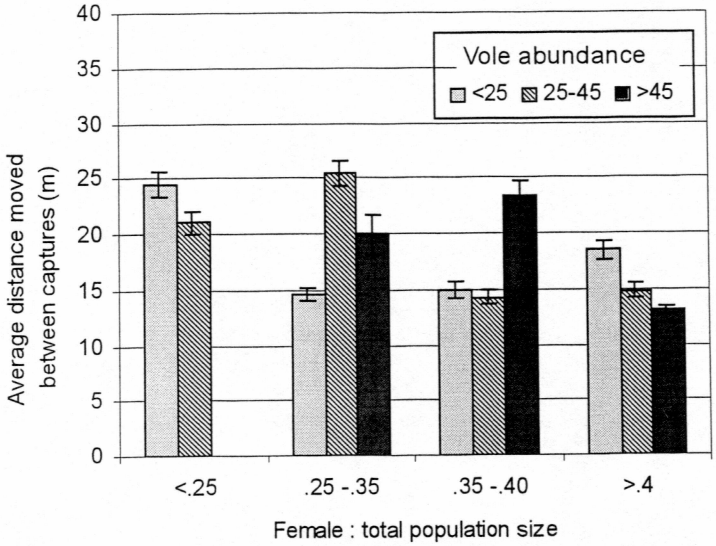


Figure 2.4. Average distance moved in meters between successive captures of 585 male *Clethrionomys rutilus* in response to an interaction between sex ratio (females : total population size) and total vole abundance. 95% confidence intervals are shown. (No data was available for the vole abundance category >45 when sex ratio was <.25).

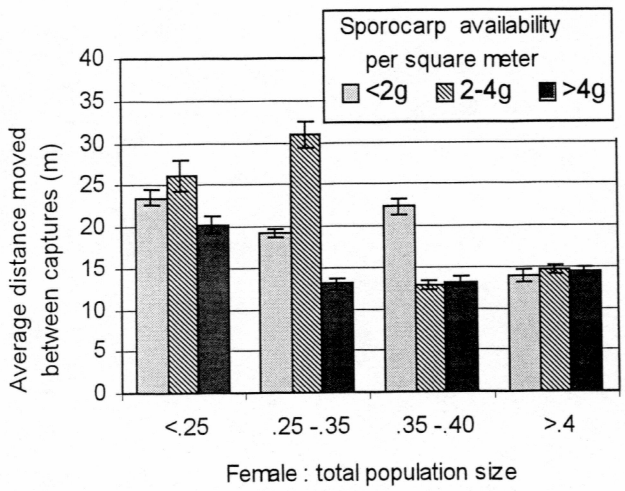


Figure 2.5. Average distance moved in meters between successive captures of 585 male *Clethrionomys rutilus* in response to an interaction between sex ratio (females : total population size) and sporocarp availability. 95% confidence intervals are shown.

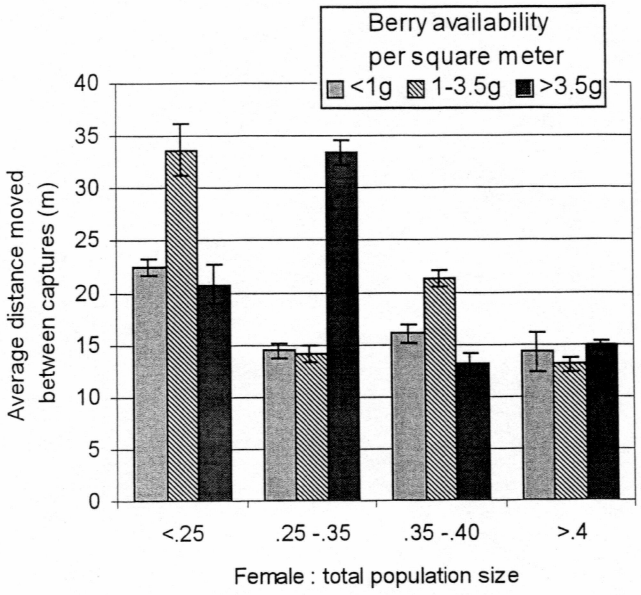


Figure 2.6. Average distance moved in meters between successive captures of 585 male *Clethrionomys rutilus* in response to an interaction between sex ratio (females : total population size) and berry availability. 95% confidence intervals are shown.

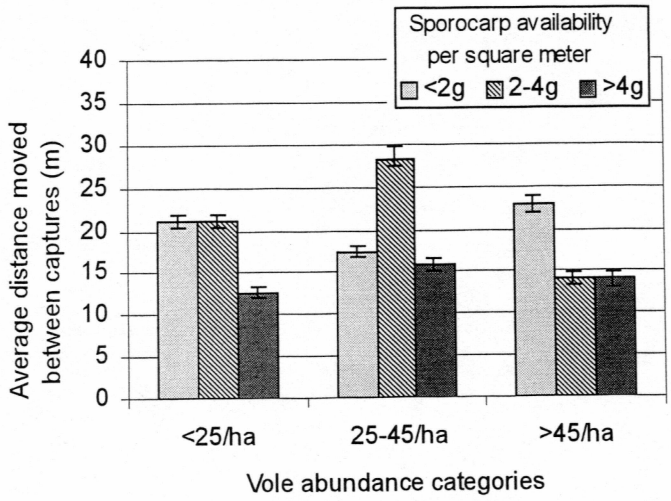


Figure 2.7. Average distance moved in meters between successive captures of 585 male *Clethrionomys rutilus* in response to an interaction between population size and sporocarp availability. 95% confidence intervals are shown.

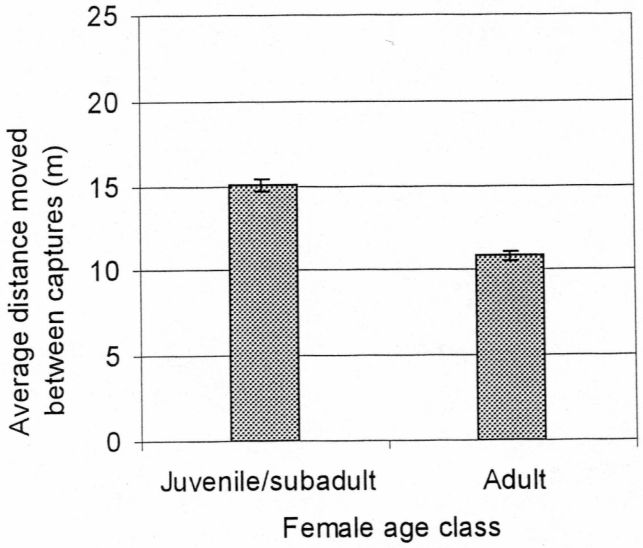


Figure 2.8. Average distance moved in meters between successive captures of 337 female *Clethrionomys rutilus* assorted into 2 age classes (juveniles/subadults and adults). 95% confidence intervals are shown.

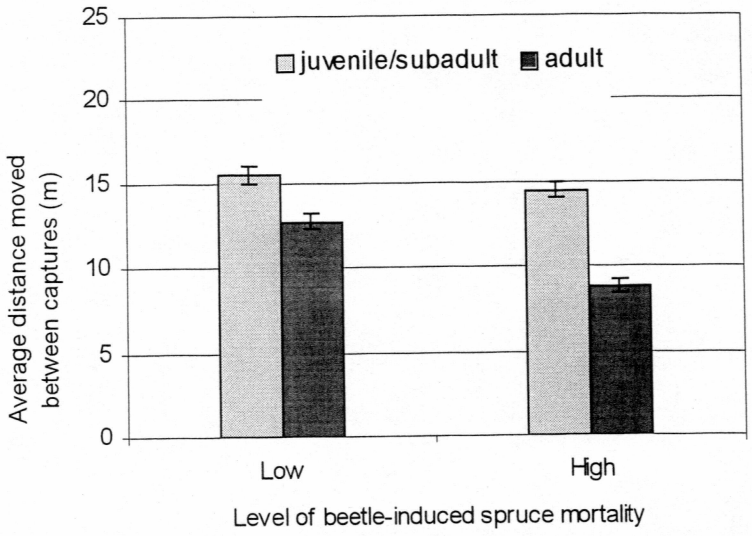


Figure 2.9. Average distance moved in meters between successive captures of 337 female *Clethrionomys rutilus* in response to an interaction between level of beetle-induced spruce mortality and female age class. 95% confidence intervals are shown.

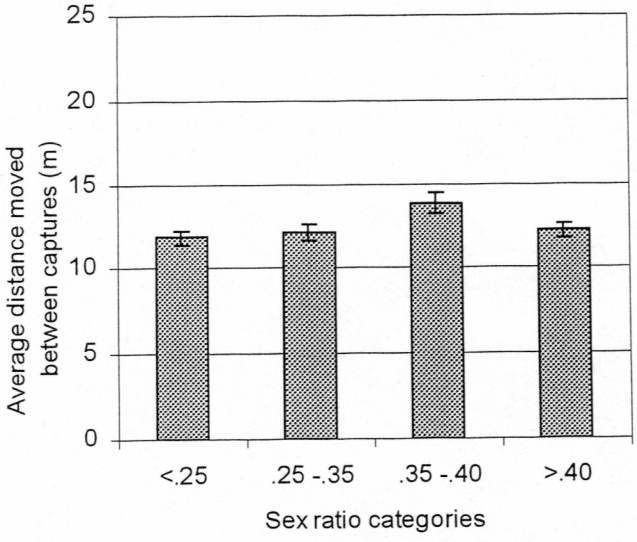


Figure 2.10. Average distance moved in meters between successive captures of 337 female *Clethrionomys rutilus* in response to 4 sex ratio categories (females : total population size). 95% confidence intervals are shown.

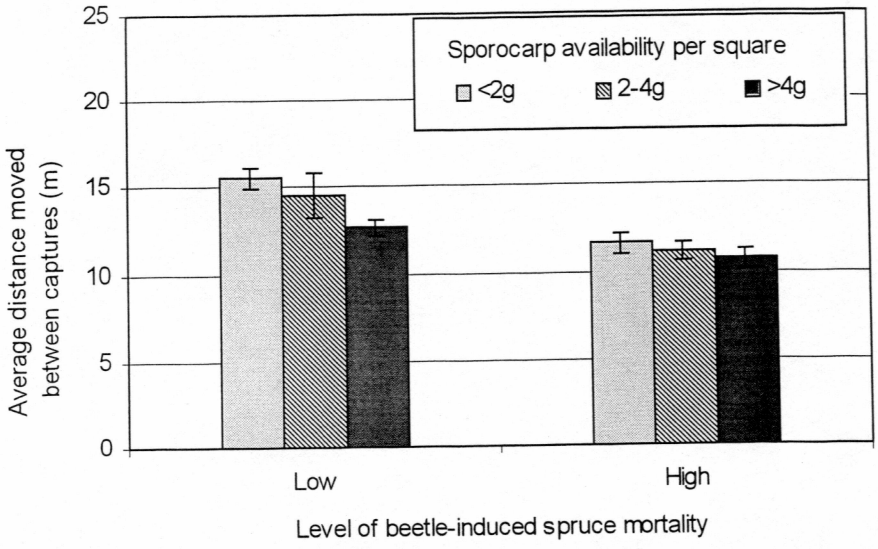


Figure 2.11. Average distance moved in meters between successive captures of 337 female *Clethrionomys rutilus* in response to an interaction between level of beetle-induced spruce mortality and sporocarp availability. 95% confidence intervals are shown.

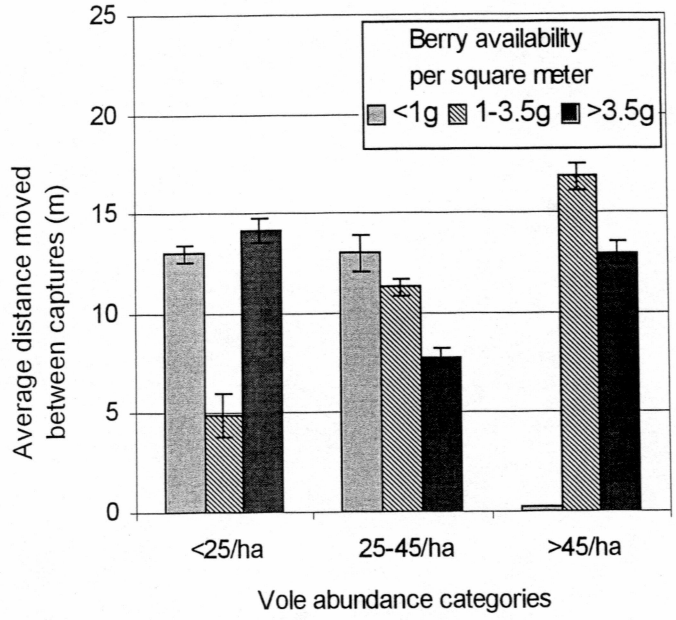


Figure 2.12. Average distance moved in meters between successive captures of 337 female *Clethrionomys rutilus* in response to an interaction between vole abundance and berry availability. 95% confidence intervals are shown. (No data was available for berry category <1 g at high vole abundance >45/ha).

Table 2.1. Six-way ANOVA model results showing significance of individual variables and interactions that influenced movements of male *Clethrionomys rutilus* (585 individuals). Movements were assessed using the average distance moved between captures. Total vole population (males + females) was used for the abundance variable. The overall model was significant ($F = 7.56$, d.f. = 49, $P < 0.001$, $R^2 = 0.41$). Shown F-statistic and P-values were produced from type III sum of squares.

Variable or interaction (*) description	F-value	*P*-value
Sex ratio	**3.35**	**0.02**
Total vole abundance	1.57	0.21
Percent beetle-killed spruce	**4.46**	**0.04**
Berry availability	0.10	0.90
Fungi availability	1.79	0.17
Vegetation cover	0.39	0.53
Sex ratio * abundance	**6.43**	**<0.01**
Sex ratio * percent beetle-killed spruce	†-	-
Total vole abundance * percent beetle-killed spruce	1.70	0.19
Sex ratio * fungi availability	**3.75**	**<0.01**
Total vole abundance * fungi availability	**4.78**	**<0.01**
Percent beetle-killed spruce * fungi availability	0.38	0.54
Sex ratio * berry availability	**2.44**	**0.03**
Total vole abundance * berry availability	1.55	0.21
Fungi availability * berry availability	0.95	0.42
Sex ratio * vegetation cover	†-	-
Total vole abundance* vegetation cover	0.41	0.52
Fungi availability* vegetation cover	0.00	0.94

† Lack of data to compute these interactions

Table 2.2. Seven-way ANOVA model results showing significance of individual variables and interactions that influenced movements of female *Clethrionomys rutilus* (186 adults, 151 juveniles/subadults). Movements were assessed using the average distance moved between captures. Total vole population (males + females) was used for the abundance variable. The overall model was significant ($F = 3.15$, d.f. = 63, $P < 0.001$, $R^2 = 0.42$). Shown F-statistic and P-values were produced from type III sum of squares.

Variable or interaction (*) description	F-value	P-value
Age	**4.29**	**0.04**
Sex ratio	**2.86**	**0.04**
Vole abundance	0.96	0.38
Percent beetle-killed spruce	0.73	0.39
Berry availability	0.05	0.95
Fungi availability	0.56	0.57
Vegetation cover	0.02	0.90
Age * sex ratio	0.73	0.54
Age * vole abundance	0.52	0.60
Age * percent beetle-killed spruce	**4.72**	**0.03**
Age * berry availability	1.69	0.19
Age * fungi availability	0.87	0.42
Age * vegetation cover	2.94	0.09
Sex ratio * abundance	0.26	0.94
Sex ratio * percent beetle-killed spruce	0.82	0.44
Vole abundance * percent beetle-killed spruce	0.03	0.86
Sex ratio * fungi availability	1.28	0.27
Vole abundance * fungi availability	0.26	0.90
Percent beetle-killed spruce * fungi availability	**3.28**	**0.04**
Sex ratio * berry availability	0.84	0.54
Vole abundance * berry availability	**3.55**	**0.03**
Fungi availability * berry availability	0.55	0.70
Sex ratio * vegetation cover	2.23	0.11
Vole abundance* vegetation cover	0.00	0.98
Fungi availability* vegetation cover	0.45	0.64